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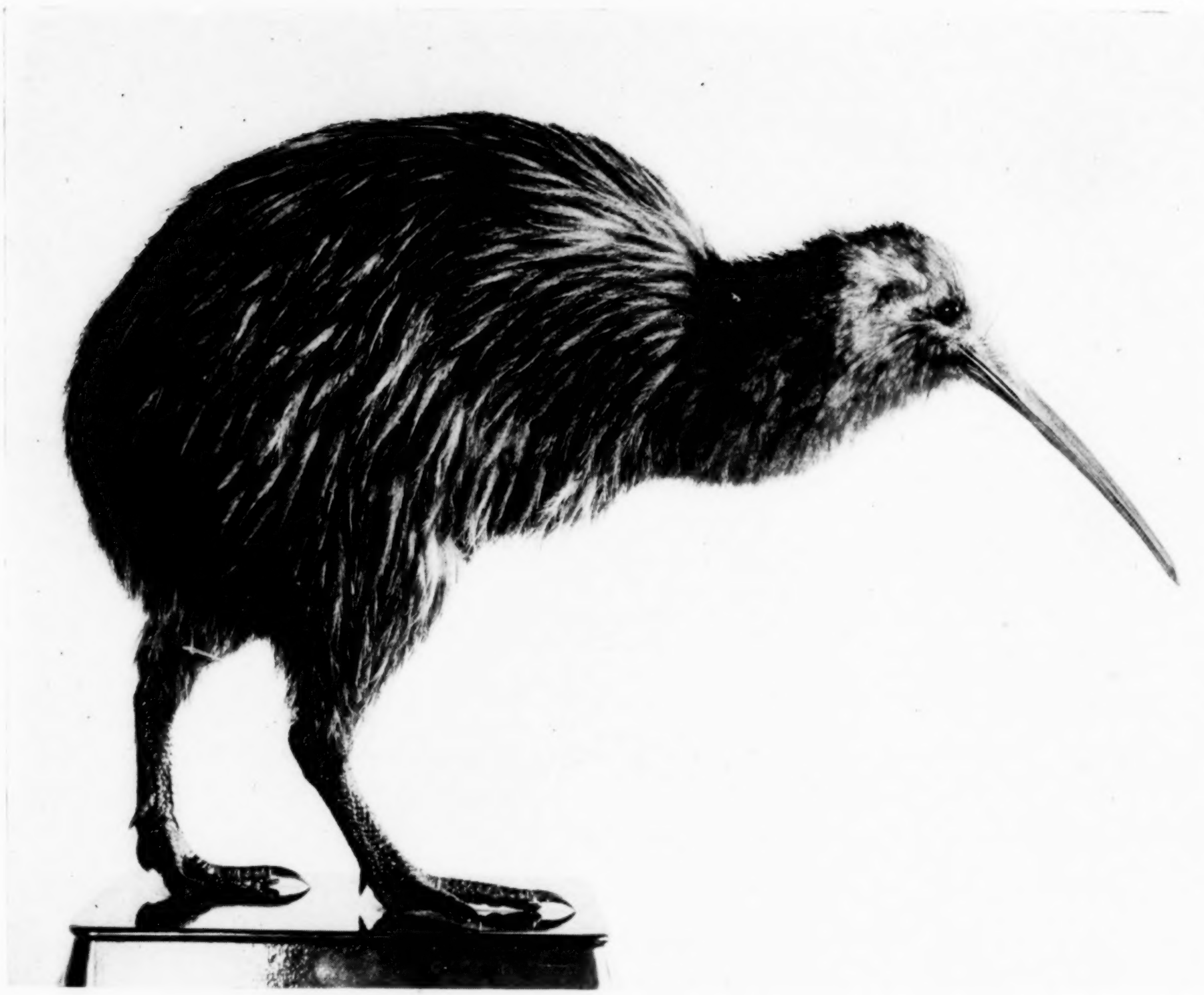
A BIRD WITHOUT WINGS



There are many birds which cannot fly, and some which have not even wings. One of these (shown above) is the Apteryx of New Zealand, called by the natives kiwi-kiwi. The most superficial observer would at once remark that this bird lacks something, since it reminds one of a man without arms; for the wings are totally absent, and the place where they should be is covered with a close smooth growth of hair-like feathers. It is known that the ancestors of the kiwi had wings, and the problem for evolutionists is how it came to lose them. August Weismann pointed out that the wings were of no use to the bird, since it lives on the ground and hunts worms by night. It has no need of wings to obtain its food; nor to escape from enemies on the ground, since there are no native mammals except bats in New Zealand. In fact, wings might be rather a hindrance than otherwise to the kiwi in moving quickly through thickets and underbrush. Birds which were born with defective wings, therefore, were not penalized by natural selection; and as variations which would spoil a complicated structure like a wing are much more frequent than those which would make it more perfect, the wings gradually degenerated until they became mere rudiments which are externally altogether invisible. Evolution works both ways, and causes improvement or degeneration, according to external circumstances. Photograph by E. R. Sanborn, New York Zoölogical Society. (Frontispiece.)

THE UTILITY OF DEATH

Evolution Could Not Take Place without It, Because the Higher Forms of Life Are so Specialized that They Cannot Change Much in a Single Lifetime— Death Therefore an Adaptation for the Benefit of the Species— the Trend of Evolution[1]

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THE question why living organisms should die is a biological question just as truly as is the question why or how they live, and it should be possible therefore to formulate in terms of the great biological processes and of the properties of living matter some general considerations on the significance of death.

If we consider the processes of organic evolution in terms of the properties of living matter we find that certain characteristics have been ascribed to all living organisms, the most important characteristics as generally given in the literature being irritability or excitability, metabolism and reproduction. Other characteristics have sometimes been given, and in the older lists, one usually noted death as one of these general characteristics. Claude Bernard insisted that "evolution is one of the most important traits of living organisms and hence of life." But whether evolution is regarded as a separate and distinct characteristic of living matter, or as the inevitable result of the operation of the other three properties, the physiologist should always keep it in mind in any discussion of general biological problems. Another property of living matter is the power of regulation of its internal conditions.

A living organism has been defined as a vortex (*tourbillon*, Cuvier) of which the direction is constant and which sweeps along molecules always of the same sort, but into which the individual molecules enter and from which they continually depart. As Goodrich has expressed it,[2] "the metabolic process in living matter draws in inorganic substances and force at one end, and parts with it at the other; it is inconceivable that these should, as it were, pass outside of the boundaries of the physico-chemical world, out of range of the so-called physico-chemical laws, at one point to reenter them at another." It is perfectly true that we cannot give an account of all of the changes of matter and energy which occur in living matter, but that is not exactly the same as saying that there are unknown and unknowable processes in living matter which never can be described in terms of changes of matter and energy. And before we can give a final account of the processes of organic evolution, we must be able to tell what are the changes of matter and energy underlying the changes of position and changes of form, which now constitute the greater part of the subject matter of evolution.

THE ORIGIN OF LIFE

The origin of living matter must go back of the origin of cells (Goodrich, p. 16) to the synthesis of organic compounds. But the precise manner of origin of these organic compounds is not for us to consider now. Let it be remembered, however, that the conditions of organic synthesis may not have been greatly different in the former ages of the earth from what they are today (Chamberlin). Further, there must have been a continuous and unbroken series of

[1] Read before the thirteenth annual meeting of the American Genetic Association on December 26, 1916, in New York City.

[2] Evolution, p. 15. London, 1912.

compounds from the earliest organic series synthesized on the earth to the living matter of the present day. The immortality of living matter dates back before the origin of the cell.

Another property or characteristic of living matter must have made its appearance here, since it is present in certain constituents of the environment (Henderson), and that is the property of regulation. I do not mean regulation in precisely the same sense in which it has been used by zoölogists and botanists to denote control of form and size and other morphological characters, but regulation of the physico-chemical conditions of the organism as well. Stability of physico-chemical conditions within certain limits is inherent in the environment, but, as has been shown, the variations may be greater in the environment than in the organism. It is characteristic of some organic compounds, and particularly of those in living matter, that slight changes in the external conditions bring about considerable changes in the compounds themselves. This is the phenomenon of irritability. Some provision for guarding against the effects of such changes on the part of those aggregates of organic compounds which formed the first stages in the evolution of living matter—a power of regulation of the internal conditions—must have been an early acquisition. The known physico-chemical properties of certain constituents of the environment afford us at least some basis for the explanation of the process of regulation in living matter (Henderson). So important for purposes of evolution is this property of regulation that I would consider it as one of the fundamental properties of living matter. We should clearly recognize then, the probability of the early participation of two fundamental properties of living matter—irritability and the regulation of internal conditions—in the evolution of living organisms. Great as have been the advantages to the individual of this property of regulation of internal conditions, its possession also entails certain disadvantages.

CONDITIONS OF LIFE

The survival of any particular complex of organic compounds, and the possibility of its further development to still more complex forms must have been dependent upon various properties, in addition to irritability and the regulation of internal conditions. The ability to form compounds of greater and greater complexity was one. The number of compounds formed, while great and varied, was subject to certain limitations because of the nature and properties of the substances entering into them. The direction of variation was subject to similar limitations, and we may imagine that orthogenesis, in a form dictated by the properties of matter and the conditions in the environment, was operative in the early stages of evolution. Early in the process of evolution, the question of fitness entered in, and we are confronted with the problem of selection. "The principle of the survival of the fittest applies with all its force to such initial steps in the evolution of life. The more completely self-regulating mixtures would outlast the others."[3] It was not many years ago when we read that "the true Darwinism, that is, the tendency which ascribes to natural selection the chief rôle in the origin of adaptations has, in Germany at least, almost no adherents."[4] But whether selection be the chief factor in the origin of adaptation or not, the operation of the principle seems clear in the early stages of evolution, and it is not readily apparent at what point in the process selection has ceased to act.

Whether or not chromosomes existed before the early stages in the evolution of living matter which led to the formation of cells, we do not know, but some of the stages in the synthesis must have been devoid of them. Some degree of heredity must have been possible in these earliest stages by other

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[3] Goodrich, *op. cit.*, p. 17.

[4] "Der eigentliche Darwinismus, d.h. die Richtung, welche der natürlichen Zuchtwahl die Hauptrolle bei dem Zustandekommen der Anpassungen zuschreibt, in Deutschland wenigstens *fast keine Vertreter mehr hat.*" Goebel, quoted by Jensen, p. 3.

means than chromosomes, for the compounds successively arising from the earlier and simpler types must have borne some resemblance to those from which they originated in qualitative and quantitative composition and general deportment. Variation must also have been present, or no evolution would have been possible.

ELEMENTS OF LIFE

It need occasion no surprise to find the primary factors of organic evolution present long before the appearance of the cell upon the earth if we but reflect a moment upon the nature of the fundamental processes or changes occurring in living matter. These are, (1) changes of form, including the visible phenomena of development and growth; (2) changes of position, including the visible phenomena of motility in general; and (3) changes of matter and energy, including all the phenomena of metabolism, and underlying all other changes in the organism. (Jost.) Changes of matter and energy must have been present from the very beginning of the evolution of living matter, since they were present in the inorganic matter from which the first syntheses of organic matter were made. I see no good reason for supposing that any radically new principle has entered in during the course of organic evolution to affect these changes of matter and energy as they are manifested in living organisms.

Herbert Spencer has shown that organisms acquire an independence of the environment. It has been shown that the mechanism by which this independence is acquired is the increasing power of the organism to regulate its internal physico-chemical conditions.[5]

It has been known for many years that the higher animals, *i.e.*, birds and mammals, had the power of regulating the temperature of the body during health. Claude Bernard noticed that the concentration of sugar in the blood remained relatively constant. And as time has gone on, it has been found that more and more of the physico-chemical conditions of the organism are regulated to a great degree of exactness. There is a regulation of the pressure, and of the distribution of the blood, of the osmotic pressure of the body fluids, of the concentration of H and OH ions in the blood (Moore) and, through this, of the activity of the neuro-muscular respiratory mechanism (Haldane). The surface tension of the blood is probably relatively constant in health (Morgan). Not all of these conditions are constant under all external conditions, but variations are in such a direction as will restore the usual condition of affairs. As Haldane expresses it, "Perhaps the most striking fact with regard to physiological phenomena is the evidence they present of activity coördinated in such a manner as to conduce towards the survival of either the individual or the species."[6]

CONSEQUENCES OF REGULATION

Certain consequences for organic evolution of this power of regulation have already been presented in various papers (Woods, Mathews, Pike and Scott). It will be sufficient simply to recapitulate here. Woods[7] has considered some of these consequences from the point of view of the effect of the environment. A clearly diminishing effect may be shown in so far as changes in the environment affect the rate of growth, the external form of the body, and the modification of mental and moral traits, as successively higher types of organisms are considered. The sex ratio in man is very constant over long periods of time and under various social and economic conditions.

It is a possible, and even probable, interpretation to say that the increasing development of the mechanisms—chemical, nervous and muscular—concerned in the regulation of internal conditions has led to the continued presence within

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[5] See the writings of Mathews, Claude Bernard, Pike and Scott, Haldane, Henderson, Huxley, *et al.*

[6] Haldane, J. S. Mechanism, Life and Personality (1914).

[7] Woods, Frederick Adams. Laws of Diminishing Environmental Influences. *Popular Science Monthly*, April, 1910.

the organism of a set of conditions which permit of, or even bring about, the optimum activity of the various cells and organs of the body under varying conditions of activity. The organism has been made more efficient.

There are other consequences, however, which should be considered more at length. These are, as I shall attempt to show, (1) the provision of a more favorable environment for the cells than exists outside the organism, permitting differentiation, (2) the possibility of an increased length of life of individual cells without undergoing division, and (3) the limitation of the possible variations occurring in the lifetime of the individual. We may take up the consideration of these various consequences in order.

1. Differentiation is possible in a high degree only when the tissues are protected from external influences. The action of enzymes upon food could not reach its highest point of efficiency if sea water passed through the digestive cavity without restriction. The case is still clearer in terrestrial forms. No such tissue as the nerve tissue of higher animals could be developed if it were continually exposed to the drying action of the atmosphere. The list could be considerably extended.

EFFECTS OF DIFFERENTIATION

But differentiation is accompanied by certain limitations of cell growth which have led some biologists to seek in it the origin of death. The conditions which have made differentiation possible would, on the basis of such a view, also be the conditions which have made the immortality of the Metazoa impossible.

There are certain objections to such a view which have apparently been overlooked. There is no inherent reason why the loss of any one general characteristic property of a cell should be accompanied by the loss of the power to divide. Gland cells in general may have lost the power of contractility, but they still retain sufficient power of cell division to give rise to tumor masses which may invade every region of the body.

Experiments on growing tissues, particularly plant tissues, in artificial culture media have shown that the cells, no matter how specialized, revert to the embryonic type—dedifferentiate as Child puts it—and from this embryonic type go on to reproduce the whole new organism. Cells can be modified if the conditions in which they develop can be modified.

Nerve cells are considered to be highly specialized cells, and their limit of division is reached sooner in ontogenetic development than is the case for other cells. Yet the number of nerve cells has continually increased as successively higher types of animals have appeared. There are more nerve cells in a monkey than in a frog, and more in the human subject than in the monkey. It seems illogical to regard as the reason for the onset of death of the cell, the limitation of cell division in a tissue which is manifesting greater numbers of cell divisions as evolution proceeds.

2. The individual cells in a higher organism in which all the mechanisms of regulation are highly developed may live vastly longer without undergoing cell division than any cells in such a long-lived form as the giant trees of California. The nerve cells in which originate the impulses leading to the respiratory movements do not, so far as I am aware, divide after birth; but from the moment of the first respiratory movement to the last breath man draws at the close of his threescore years and ten, these cells continue to function under all conditions of rest or activity.

3. The limitation of the magnitude of possible changes during the life of any one organism is a direct consequence of the development of a high degree of regulation. This limitation covers the chemical constitution of the organism, since variations beyond certain narrow limits are incompatible with continued existence. The higher organism either maintains its constancy of conditions under all variations of the external environment or dies when an adjustment is no longer possible. There is also a limitation of structural changes. Unrestricted growth of any organ or tissue in the body interferes with the general equilibrium; the efficiency of the

organism is impaired and frequently death results.

HEREDITARY LIMITS

The limitation of changes in the central nervous system in all probability sets a limit to man's achievements during his lifetime. And in no case is a sufficient amount of change possible in the lifetime of any higher organism, no matter how prolonged, to lead to the development of new genera or species.

It is man's nervous system which has raised him above the animals, and on which his progress for the future depends.[8] Limitation of change in this system probably means a limitation of personal achievement, and would mean a limitation of the achievement of the race if no progressive change through the production of new individuals were to occur. Changes of sufficient magnitude for purposes of organic evolution can occur only through the cumulative effects, persisting through many generations, of the small changes, always toward something better if the race or the species is to endure and take its place in the hierarchy of organic life, appearing in each successive generation of new individuals. The immortality of all individuals which have ever appeared upon the earth would have resulted in an insufferable congestion and a ferocity of the struggle for existence which would transcend anything we now know. Ferocity does not seem to be now, nor to have been in the past, the sole object of evolution.

The development of the metazoan body has led to the greater independence of the organism and greatly increased its efficiency. But the coordination of all activity has led to the development of a rigid physico-chemical and anatomical basis in which change is limited during the lifetime of the individual. The restriction of cell division is a necessary consequence of the regulation of body form just as the restriction of changes of chemical constitution is a consequence of the regulation of physico-chemical conditions within the organism. The restriction of cell growth extends even to the germ cells, since uncontrolled development of such cells within the body would lead to disaster exactly as uncontrolled development of epithelial or glandular or connective tissue in malignant growths finally leads to the death of the organism. The germ cells of higher organisms have lost the power of parthenogenetic division, and develop only under such conditions as will decrease, in large measure, the danger to the parent organism. The limitations to possible change during the lifetime of any individual preclude changes of sufficient magnitude for purposes of evolution. The death of the unmodifiable organism may be considered as an adaptation[9] from the point of view of the species.

The Evidence of Evolution

THE THEORY OF EVOLUTION, with special reference to the evidence upon which it is founded. By William Berryman Scott, Blair Professor of Geology and Paleontology in Princeton University. Pp. 183, price $1.00. New York: The Macmillan Co., 66 Fifth Avenue, 1917.

Dr. Scott thinks it is desirable for students beginning work in science to know on what evidence the theory of evolution is based, instead of accepting it meekly as an unquestionable dogma; and in a simple manner he has considered the present status of the question; the evidences from classification, domestication, comparative anatomy, embryology, blood tests, paleontology, geographical distribution, and experimental breeding. The latter chapter is weaker than the others. But as a whole the book is commendable; it ought to be very useful to beginners who want a survey of the whole question, for most of the accepted text-books that are comprehensive are out of date.

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[8] See Pike, F. H. Dr. Gaskell's Work on Organic Evolution. *Science*, December 4, 1914.

[9] The idea of death as an adaptation was put forth by Aug. Weismann, on somewhat different grounds than those above outlined, in 1881. His lecture, Ueber die Dauer des Lebens, was printed in 1892 in his *Aufsatze über Vererbung*. See also Gardiner, "Weismann and Maupas on the Origin of Death," *Marine Biological Lectures*, 1890, Boston, 1891, p. 107.

PROTECTIVE COLORATION IN SEEDS OF BOLIVIAN MAIZE

Each Seed Ordinarily Infested by Not More than One Larva—Mottled Seeds Look as if They Had Already Been Entered, and Therefore the Larvae Appear to Discriminate against Them

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PROTECTIVE coloration in animals is familiar, but in plants it is not so common. What may be a case of protective marking has been found recently in a shipment of maize from Bolivia.

In a collection of maize secured from the Bolivian exhibit at San Francisco in 1915, through the courtesy of Dr. Otto Buchtien, an ear was found with kernels that had the color of the aleurone cells distributed in a curious mottled pattern strongly suggesting the appearance of self-colored seeds that had been infested with the larvae of the Angoumois grain moth (*Sitotroga cerealella*).

The possibility of this resemblance serving as a protection against the Angoumois moth was immediately suggested. Several investigators have recognized that two larvae do not enter a kernel of wheat or other small grains, but so far as known this fact has not been established for maize. The fact that a single larva completely consumes the contents of one of these small grains may account for the fact that they usually support but one larva. A seed of maize, however, is large enough to provide ample food for two or more, and unless some selection is exercised by the larva many seeds should be found having more than one occupant.

As the eggs of the Angoumois moth are laid in batches of about thirty, the discrimination in the choice of seeds must be made by the larvae.

If selection is exercised it does not seem unreasonable to suppose that the track in the aleurone layer serves as a warning to the newly hatched larva that the kernel already has an inhabitant, and it seems possible that the mottled seed sufficiently resembles the track of a larva to accomplish the same result.

The mottled ear was shelled and the number of infested seeds determined. There were 202 undamaged seeds and 100 with a single larva, but none was found with more than one larva.

As further evidence that larvae avoid seeds already occupied, a census of the self-colored ears from the same collection is shown in Table I. If the selection exercised by the newly hatched larvae were perfect no seeds having more than one inhabitant should be found, while the table shows many such seeds. The number, however, is far short of that which might be expected had there been no selection. Some degree of selection, then, would seem to be a fact, and newly hatched larvae do avoid seeds already inhabited.

If it is admitted that the white tracks left by larvae deter other larvae from entering the seed, it does not appear too fanciful to suppose that the white mottling which so closely resembles the tracks, serve the same purpose. The idea is strengthened by the small percentage of infested seeds and the fact that none was found having two inhabitants. It is, of course, possible that the mottled ear was more favorably situated and hence was not subjected to the same severe attacks. This chance, however, is remote as the remaining ears of many types that occupied the same case were all badly infested.

A comparison of the degree of double infestation on a self-colored ear having all the seeds infested, with the degree

SEEDS OF BOLIVIAN MAIZE

The group at the left is made up of self colored seeds infested by the larvae of the Angoumois moth, whose tracks are conspicuous on the seeds. The group at the right has not been attacked by this larva, but the mottled coloring resembles the tracks of the larvae. It seems possible that this mottling may deceive the larvae; they "think" that the seeds have already been entered and therefore pass on to find fresh fields. Photograph natural size. (Fig. 1.)

TABLE I.—*Percentage of Non-infested, Single-infested and Double-infested Seeds Compared with the Expected Percentage**

Color of ear	Total seeds	Per cent of seeds not infested	Per cent of seeds infested with one larva	Per cent of seeds infested with more than one larva	Expected more than one larva	Deviation	$\frac{D}{E}$
Self	410	26.8	66.0	7.1	19.3±1.31	12.2	9.3
Self	295	33.9	61.3	4.7	15.9±1.44	11.2	7.8
Self	254	1.6	74.8	23.6	34.5±2.01	10.9	5.4
Mottled	302	67.0	33.0	.0	4.4± .8	4.4	5.5

* I am indebted to Dr. Sewall Wright for suggesting the method used to determine the expected number of double-infested seeds.

The formula for calculating the expected percentage of uninfested seeds is $\left(\frac{N-1}{N}\right)^L$ and for the percentage of single-infested the formula is . . . $L\left(\frac{N-1}{N}\right)^{L-1} \cdot \left(\frac{1}{N}\right)$ where N = the total total number of seeds and L = the number of larvae. The remainder, of course, equals the number of seeds infested with one or more larvae.

of infestation on a mottled ear, also affords a measure of the effectiveness of the mottled aleurone as a protection. Since all the seeds of a mottled ear have the appearance of being infested the percentage of seeds actually infested should approximate the percentage of double-infested seeds on a self-colored ear having all the seeds infested by at least one larva. These

ears would appear alike and discrimination would be impossible.

One all-colored ear having practically all of the seeds infested is shown in Table 1. The percentage of double-infested seeds on this ear is $23.6 \pm 2.1\%$ while the percentage of infested seeds on the mottled ear is $33.2 \pm 1.8\%$. If this difference is considered significant, it will be necessary to look upon the protection afforded by the mottled color as not quite so effective in preventing initial injury as actual infestation is in preventing double infestation. In other words the mimicry is not quite perfect.

It would be interesting to compare the degree of infestation of mottled seeds with seeds entirely white, but no white ears of the mottled type were present in the collection, and an examination of several importations received directly from Bolivia in previous years revealed no all-white ears of this type.

The moth *Sitotroga cerealella* first attracted attention in Europe in 1728 and is supposed to have reached this country about thirty years later. Of its occurrence in Bolivia nothing seems to be known. The fact that the ancient Incas were accustomed to store large quantities of corn might seem to indicate that the insect was not present. It would appear, therefore, that although mottled seeds may be in some measure protected, it would be quite unwarranted to ascribe the development of the mottling to selection. It must be remembered that the degree of protection which the mottling of the seeds seems to afford may after all be but the result of accident. The resemblance is so close, however, that the possibility of its affording protection seems worth considering. A true test will await an ear having both self-colored and mottled seeds, a combination which is genetically possible.

Experience with Loganberry Hybrids

W. O. Backhouse's remarks on loganberry seedlings (JOURNAL OF HEREDITY, November, 1916), mentioned experiments made by Laxton Bros. in England. Notice in the *Gardeners' Chronicle* (London), evoked a communication (December 23) from Laxton Bros., in which, after stating that they are "substantially in agreement" with Backhouse, they say:

"In the last paragraph you make reference to the Phenomenalberry as being of undoubtedly hybrid origin. We are firmly of opinion that this is nothing more nor less than a seedling from the Loganberry, which it very closely resembles, although slightly larger and sweeter—in fact, the difference is so small to the eye that we do not think we could pick out the plants from the Loganberry unless they were in the fruiting stage. You also figure the Lowberry as being a hybrid between the Loganberry and the Blackberry. We do not think this is a fact. We ourselves have imported a variety under the name of Californian Mammoth Blackberry, from America, which we are unable to distinguish from the Lowberry. We draw your attention to these matters, as when your paper makes authoritative statements they are apt to be quoted in years to come. There are undoubtedly two Rubus hybrids in commerce, namely, the Mahdi (between a yellow Raspberry and the Loganberry) and the Laxtonberry. We have obtained F_2 seedlings from the Mahdi—amongst them a Rubus similar to a yellow raspberry—and the Laxtonberry is a cross between Superlative Raspberry and the Loganberry. Both these hybrids are more or less self-sterile, and require planting amongst other Rubi. We have purchased from Messrs. Veitch the stock of the Veitchberry, which is a hybrid between the Blackberry and the Loganberry. This is not at present in commerce. There have been many seedlings from crosses between the Loganberry and other Rubi, but in nearly all cases self-sterility has prevented them being of any commercial value."

SELF-STERILITY

In Some Cases Where a Plant Cannot Be Fertilized by Its Own Pollen, It Appears That the Pollen-Tube Finds a Very Suitable Medium for Its Food Supply, and Hence Does Not Grow Long Enough to Ensure Fertilization

C. W. Moore

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SEVERAL who have made a study of the problem of the inheritance of self-sterility of plants have obtained results which did not point to any one definite manner in which flowers act when self-pollinated. In this work the purpose was to try to find some clue to the nature or cause of self-sterility. Several different kinds of plants that had been reported self-sterile were grown, and the stigmas and styles were examined.

In order to avoid confusion, the term "self-sterility" will here be understood to mean that the pollen of a flower is not capable of fertilizing the ovules of that flower, but that the pollen is capable of fertilizing the ovules of another plant and that the ovules of the plant are capable of setting seed when pollinated with pollen from another plant. Thus flowers which have either pollen or ovules which are abortive would not be confused with plants that have self-sterile flowers.

The kinds of plants that were used were Tradescantia, alsike clover (*Trifolium hybridum*), alfalfa (*Medicago sativa*), and the Shirley poppy (*Papaver rhoeas*). The flowers from twelve plants of Tradescantia were used. There were three plants of *T. occidentalis*, and nine that were F_1 generation hybrids from a cross of *T. occidentalis* by *T. pilosa*. On the twelve plants, eighty-three self-pollinations were made, but none of them set seed. Twenty-six cross-pollinations were made, and all of them produced seed.

An examination of the styles of twenty pistils that were cross-pollinated showed pollen tubes running to the base of the style. The pistils were examined by crushing under a cover-glass. Then a drop of 1% solution of gentian violet stain was added. The pistil was left in the stain for about one minute, and then the excess of stain was washed off. The pollen tubes could easily be distinguished since they contained many small vacuoles and had no cross walls. The stigmas of the self-pollinated flowers showed good germination of pollen when examined in the same manner; however, the pollen tubes did not grow down the style. The styles of thirty self-pollinated flowers were examined, and the longest pollen tube was found to be 0.5 mm. in length. The style of Tradescantia averages about 5.0 mm. in length. Thus, apparently, the reason for the self-sterility of Tradescantia is due to the failure of the growth of the pollen tubes after germination.

A SIGNIFICANT DIFFERENCE

The significant fact about the pollen tubes from a self-pollination was that they were much wider than those from a cross-pollination. The average diameter of fifty pollen tubes from the self-pollinations was .0216 mm., while the average diameter of fifty pollen tubes from the cross-pollinations was but .0144 mm. The measurements of the pollen tubes were taken as close as possible to the pollen grain. Measurements of the diameter of the pollen

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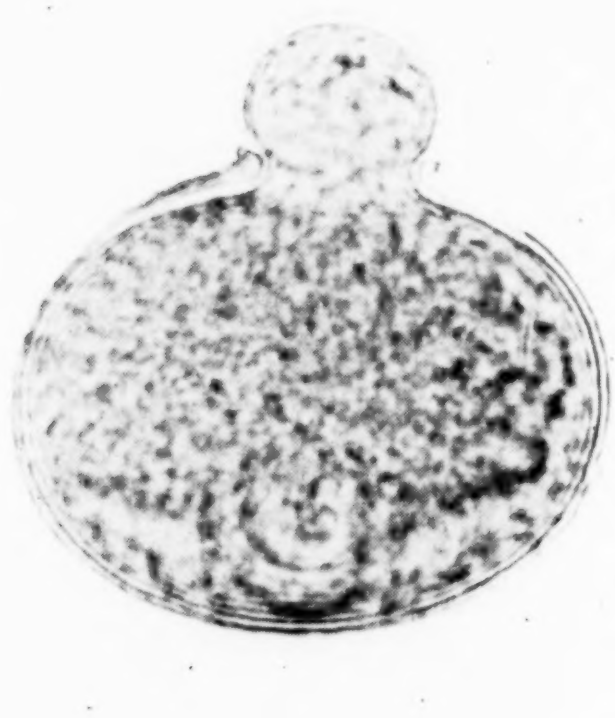
[1] Paper No. 56 of the Department of Plant-Breeding, Cornell University. Read at the thirteenth annual meeting of the American Genetic Association, December 27, 1916, in New York City. The writer wishes to express his appreciation of the many helpful suggestions and useful criticism received from Prof. E. E. Barker.

tubes from cross-pollinations were taken after they had grown down the style; they averaged .013 mm. Thus the width of the pollen tubes in a cross-pollination was nearly constant, being slightly larger near the pollen grain. The largest diameter of a pollen tube in a self-pollination was .028 mm., while the smallest was .016 mm. The largest diameter of a pollen tube in a cross-pollination when the measurement was taken close to the pollen grain was .024 mm., while the smallest was .012 mm. When the measurements of the pollen tubes from the cross-pollinations were



POLLEN GRAIN "BUDDING"

When the pollen grain falls on the stigma of a female blossom, moisture and chemical reactions make it germinate. Part of the contents push their way through a pore in the wall, as shown above in a photomicrograph of sweet-pea pollen by John Howard Paine. (Fig. 2.)

taken down the style, the diameters were also .024 mm. for the largest and .012 mm. for the smallest. Thus the greater width of the pollen tubes from a self-pollination is not so great as to cause any mechanical difficulty to its growth down the stylar canal, since the smallest tube from a self-pollination was of the same size as the largest one of a cross-pollination which was measured down the style.

With alsike clover (*Trifolium hybridum*) fourteen different plants were used. There were 1,437 cross-pollinations and 1,452 self-pollinations made on these plants. They were covered with a netting so that the pollinations could not be worked upon by insects. A number of flowers under the screen were left untripped and a number of flowers on plants outside of the screen were left to be open-pollinated. The following table shows the percentages of flowers set in the different pollinations.

	Total No. of flowers pollinated	*No. of flowers setting seed*	*Per cent of flowers setting seed*
Cross-pollinations..	1,437	309	21.50
Self-pollinations...	1,452	40	2.75
Flowers not tripped	3,394	1	0.02
Open-pollinated...	3,480	2,442	70.17

In making a self-pollination the flower was tripped by a pair of tweezers and no care was taken to prevent pollen from one flower in a head from pollinating another flower of the same head. In making the cross-pollinations, the flowers were not emasculated and the pollen from another plant was dusted on to the stigma, using four or five flowers to pollinate a head.

A number of cross-pollinated styles were examined in a similar manner as with Tradescantia, and in all cases there was a large number of pollen tubes growing throughout the length of the style. The styles of forty self-pollinated flowers were examined. There was good germination on all of the stigmas, but on thirty-nine of the styles examined no pollen tubes were found to extend over 1 mm. down the style. In one style of the forty examined, three pollen tubes extended the whole length of the style. This probably accounts for the low percentage of flowers set from the self-pollinations.

With alfalfa (*Medicago sativa*) the flowers from eight different plants were used. The self and cross-pollinations were made in the same way as with alsike clover. The following table gives the number of flowers and the percentages:

	Total No. of flowers pollinated	*No. of flowers set*	*Per cent of flowers set*
Cross-pollinations..	822	318	38.7
Self-pollinations...	1,459	396	27.1

Thus a larger percentage of the flowers was fertilized from the cross-pollinations than from the self-pollinations. From this, alfalfa may be said to be partly self-sterile.

With the Shirley poppy (*Papaver rhoeas* var. *Shirley*), there were eighty-six flowers self-pollinated, using sixty-eight different plants. There were seventy-five flowers cross-pollinated, using seventy different plants. The following table gives the results of the pollinations.

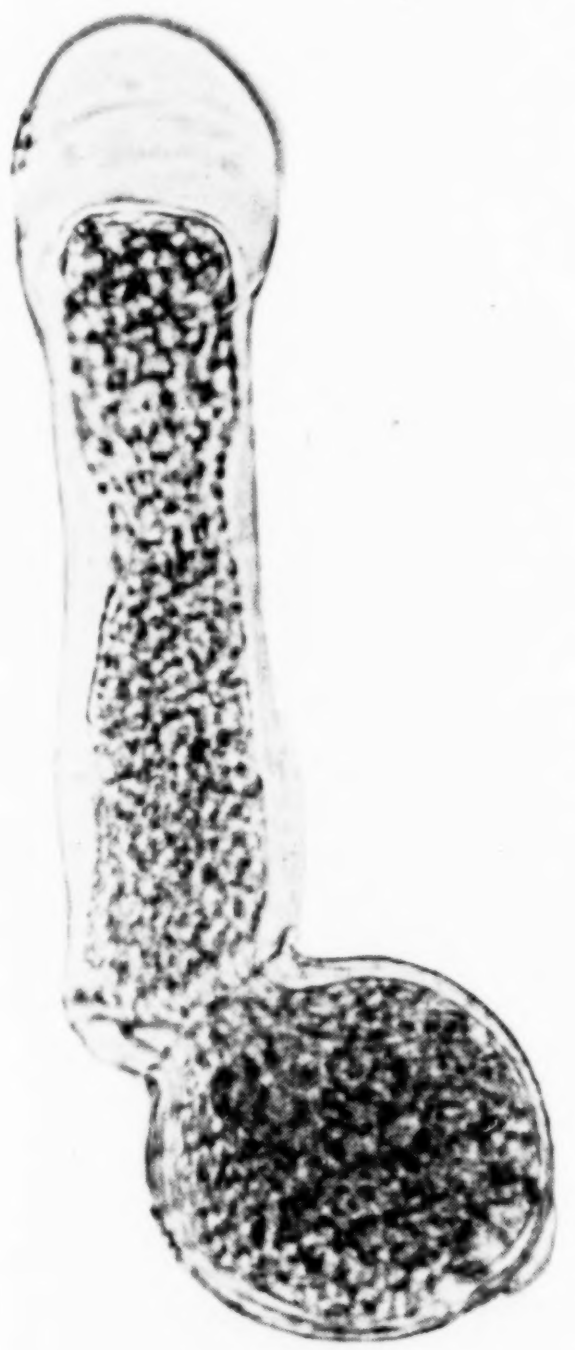
	Average number of seeds set per capsule	*Percentage of flowers yielding 1 or more seeds*
Cross-pollinations....	643.5	84.0
Self-pollinations.....	79.7	39.5

For cross-pollination, the flowers were emasculated about two days prior to the opening of the flower. All flowers were bagged with glacine bags. Since but 84% of the cross-pollinations set seed, it suggests that a number of plants may have been cross-sterile. However, this cannot be definitely stated until the work is again checked up as considerable experimental error may be involved, tests of the germination of pollen on each stigma not having been made. However, on all of the stigmas from cross-pollinations that were examined good germination of pollen was observed.

The species of Tradescantia, alsike clover, alfalfa, and Shirley poppy showed different degrees of self-sterility. Tradescantia was completely self-sterile; in alsike clover about 2% of the flowers set seed when self-pollinated; in alfalfa 27% of the flowers were fertilized with self-pollen, and when the Shirley poppies were self-pollinated 39% of the flowers set seed.

FUNCTION OF POLLEN TUBE

From a morphological standpoint, the pollen tube of the angiosperms has two functions; first, the transferring of the male generative nucleus to the embryo sac, and second, the function of growth which is one of food assimilation. The pollen tubes of the Cycadales of the gymnosperms are much branched and according to Coulter (1910, p. 201) always function as an absorptive organ. They do not have the function of transferring the male nucleus since this cell is a swimming sperm. In the higher groups of the gymnosperms and angiosperms, the nucleus loses the power of motility and the pollen tube has taken on the function of transferring the nucleus to the embryo sac. In the manner of assimilating food and growth, the pollen tube acts in a similar manner to the mycelium of a fungus.



THE TUBE GROWS

Constantly absorbing nourishment from the surrounding tissues, the tube grows longer with great rapidity. It may be that its elongation is due to the need of seeking farther for food, and that if the food supply around it is very suitable for assimilation, it will grow wide as in the case of Tradescantia instead of long. This hypothesis has been advanced to account for cases of self-sterility. Photomicrograph by John Howard Paine. (Fig. 3.)

Compton (1913, p. 200) has suggested

A LONG TUBE

While the above pollen tube is long as compared with the one beside it, which is just beginning to germinate, it has by no means reached the maximum length. In maize, the pollen grain falls on the end of the "silk" and must grow all the way down that to the seed, a distance of a foot or more in many cases. When it is remembered that the pollen grain is not much larger than a particle of dust, and sometimes can hardly be seen without a microscope, its great capacity for growth will be appreciated. Photomicrograph by John Howard Paine. (Fig. 4.)

that self-sterility in plants may be analogous to wheat which is immune to the rust fungus. The rust fungus is an obligate parasite and when the spore germinates on the host the mycelium penetrates the tissue. In the immune plants the tissue is immediately killed. Since the fungus is an obligate parasite, it cannot grow in the dead tissue of the host and so dies. Thus the plants which are immune are very susceptible to the fungus. When this analogy is applied to self-sterility, it may mean that the pollen tube from a self-pollination is in a more favorable medium for food assimilation. Since the primary function of the pollen tube is to assimilate food, it does not continue to grow at so fast a rate as a pollen tube from a cross-pollination where the medium is not so suitable to it. The pollen tube from a cross-pollination is assumed to continue growth in order to obtain a better food supply.

It is possible to interpret the greater width of the pollen tubes from a self-pollination of Tradescantia in two ways. First, there may be an inhibitor either in the pollen grain or stigma which inhibits the growth of the pollen tube from a self-pollination; and since the pollen tube cannot lengthen itself, it grows wider. Or, second, the food supply may be more favorable and so the tube has not the incentive to prolong itself.

CORRENS' HYPOTHESIS

Taking the first alternative, Compton (1913, p. 203) has shown that the inhibitor hypothesis as put forth by Correns (1912) does not explain the phenomenon of self-sterility. Correns worked with *Cardamine pratensis*, and he assumed that self-sterility was due to two allelomorphic inhibitors, the presence of either being able to cause self-sterility. Correns made crosses between plants which, according to his hypothesis, should have given him four classes of progeny, one of which should lack both inhibitors and so be self-fertile. However, all of the plants were self-sterile, so that the experimental evidence obtained by Correns did not confirm the hypothesis.

East (1915, p. 85) suggests that the

action of the stigma to a pollen tube from a cross-pollination may be different from that to a pollen tube from a self-pollination. He states that "all gametes having in their hereditary constitution something different from that of the cells of the mother plant, however, can provoke the proper secretion to stimulate the pollen tube growth, reach the ovary before the flower wilts, and produce seeds." From this it may be inferred that there may be an enzyme in the pollen grain that in a cross-pollination is able to induce the stigma to excrete a stimulating substance so that the pollen tube is able to grow. In a self-pollination this enzyme is not able to act. However, if this were the case, when a few cross-pollen grains were placed on a self-pollinated stigma, they would be expected to germinate and cause the stigma to produce the stimulating substance. Thus the pollen tubes from the self-pollination would also benefit by the stimulating influence and should be able to grow and bring about fertilization. However, the work with alsike clover does not support this hypothesis. It must be assumed that if any pollen tubes were able to grow that it was due to this stimulating influence. As a fact, three pollen tubes from a self-pollination of alsike clover grew throughout the length of the style while the other tubes remained short. If this enzyme hypothesis were to be accepted, the same stimulus which made the three pollen tubes grow should also have made the other pollen tubes grow.

EFFECT OF FOOD SUPPLY

The second alternative may be taken, namely, that the greater width of the self-pollinated pollen tubes of Tradescantia is due to the fact that the food supply is more favorable to the nourishment of a self-pollen tube than it is to a cross-pollen tube. On account of the abundant food supply the pollen tubes did not lengthen, but grew wider since they were in a very favorable medium. By this hypothesis it is possible to explain most of the data here presented in regard to self-sterility, and it is not contradictory to any cytological evidence. The Shirley poppy results showed that a small proportion of the plants were probably cross-sterile. However, this is only reasonable since if a large number of plants were used, a few of them would be expected to have nearly the same kind of food supply and so be cross-sterile. East (1915, p. 81), working with *Nicotiana*, and Stout (1916, p. 384) with *Cichorium intybus* also found a small percentage of plants to be cross-sterile.

Thus the hypothesis suggested by Compton (1913, p. 200) that self-sterility in plants may be analogous with wheat which is immune to the rust fungus, seems very probable. Briefly, the main evidence favoring such an explanation is as follows: (1) The primary function of the pollen tube is to obtain food. (2) The method of obtaining food and manner of growth are similar to a fungus. (3) Pollen tubes of self-pollinations of Tradescantia were about one-third wider than those of cross-pollinations. (4) If a number of pollen tubes grow throughout the length of the style, other pollen tubes in that style may remain short. However, this explanation is only tentative, and much more data should be obtained before it can be held that this is the correct solution.

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COEDUCATION AND EUGENICS

Women Graduates of Syracuse University Have Very Low Marriage and Birth Rates Those of Men Graduates Are Much Higher Colleges Perhaps Receive an Abnormal Type of Woman and Nature of Education Can Effect Little Change in her Unmarriageable Character.

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WHILE considerable work has been done recently in the statistical study of the fecundity of college graduates there are still some phases of the subject for which the facts and figures have not been fully presented. Most of the work heretofore has been based on the records of the separate colleges for men and women and, aside from some data as to marriage rates, no extensive study has been made of any coeducational institution. To supply this deficiency the writer undertook nearly a year ago a compilation of the statistics of Syracuse University, but has been delayed in publishing the results by the press of other work.

The finding of previous investigators has been, in general, that college graduates show a declining rate of fecundity to a point where they are not even reproducing themselves, and that the record for the graduates of women's colleges is by far the lowest. This has led to severe animadversions upon the "atmosphere" of the separate college for women with strong intimations that coeducational schools would render a much better showing. The work here presented was undertaken with the expectation that it would furnish confirmatory facts for so plausible a theory. If the figures have failed to sustain the claims for coeducation it cannot be charged that it is due to any bias on the part of the compiler. The results obtained seem to demand a theory of selection which has been recently intimated but not presented definitely as an explanation of the low birth rate seemingly fostered by the higher education of women.

The tables here presented are condensed summaries of more elaborate statistics. The work has been based on the *Alumni Record and General Catalogue of Syracuse University* edited by Dean, now Vice-Chancellor Emeritus, Frank Smalley, an elaborate work in two volumes published in 1911. The period covered by the statistics is exactly fifty years from 1852 to 1901, inclusive. It is obvious that later figures would be of doubtful value. In fact even the data recorded for the decade 1892 1901 should be used with some caution as in the later classes of this decade there may be some children and even a few marriages not yet recorded. We feel confident, however, that these will never materially affect our conclusions and will scarcely produce an appreciable effect in the averages. We have the records for ten years a ter the graduation of the last class while the average interval from graduation to marriage is for the men 4.5 years and for the women 4.7 years.

EARLY HISTORY OF SYRACUSE

Why the statistics are carried back to 1852 while the University is commonly understood to have been founded in 1871 may need some explanation. Prior to 1871 the institution had existed as Genesee College at Lima, N. Y., having been a coeducational school from the beginning and with the same collegiate ideals. In the latter year faculty and students were transferred to the city of Syracuse and reorganized as Syracuse University, the alumni of the old college being formally granted degrees from Syracuse in order to obviate any question as to their legal standing in the new institution.

The tables here published have been compiled separately for the men and the

women, and have been arranged by decades, this being a convenient period of time and also permitting the segregation of the statistics for the two phases of the institutional life, the first two decades covering Genesee College and the last three belonging strictly to Syracuse. It is evident that at the time of transition there is no marked differentiation in the statistics, a fact which confirms our belief that there was no essential break in the continuity of the institutional life.

In compiling the figures only those students who graduated in liberal arts courses were considered. Figures for non-graduates would be interesting for comparison especially in the case of the women, but the records do not give the later history of this group. The restriction to liberal art work seemed necessary in order that the results might be comparable with statistics previously published for men's and women's colleges. Prior to 1873 there were no fine arts students, but after that date they increased rapidly, and it must be remembered that in the last two decades covered by our figures there was a considerable body of women in fine arts work, many of whom became the wives of the men in the liberal arts college. This has bearing on one of our categories as will be seen later.

STUDENT BODY HOMOGENEOUS

Naturally the first comparison to be made is between the two tables. In this case we have two populations differentiated in only the one factor of sex. Both men and women were drawn from the same social strata. This was particularly true of the liberal arts college. There were students of both sexes from homes of wealth, at least sufficient to provide for all their necessities; there were some in straitened circumstances demanding close economy; and there were yet others really struggling with poverty. In each class there were apparently as many women as men in proportion to the total number of each in the college, so far as one could judge who was intimately acquainted with the student life of the institution. The college environment, at least in the last two or three decades, was absolutely uniform. The students of both sexes roomed largely in private houses in the vicinity of the college or in a few fraternity club-houses and took their meals at private boarding houses or students' clubs. There were no dormitories, no matron or dean of women, and the young women were under no more surveillance as to conduct and social liberties than the young men; for many there was doubtless a larger liberty in social life than they had been permitted to enjoy at home. The two sexes met in the same classrooms, heard the same lectures, and recited in each other's presence.

The first point to be considered in a comparison of the two sexes is the proportion that marry. In the earlier decades the numbers involved are so small that considerable variation in averages or percentages is probably of no great significance. Both sexes seem at first to have maintained a nearly equal frequency of marriage, but in the later decades there is a remarkable falling off in the percentage of women who marry, and, for the whole period, we have only 57% of the women as compared to 81% of the men. The significance of this, if any, we will leave for later discussion.

The next item in the table, "Average age at marriage," need detain us but briefly. There appears nothing peculiar about it. The women average about a year younger than the men and the figures appear remarkably uniform especially for the young men. In view of the fact that during the period covered the amount of preparation required of young men for professional life has steadily augmented, it seems remarkable that there has not been an advancing average age at marriage. This has commonly been predicated, but our figures do not support the hypothesis. They sustain the deductions of Phillips as to similar conditions at Harvard and Yale.[1]

[1] Phillips, John C. A Study of the Birth Rate in Harvard and Yale Graduates. Harvard Graduates Magazine, 25: 25–34. Reprinted in part in the JOURNAL OF HEREDITY, 7: 565–569.

The next subject is of special interest as viewing from a new angle that perennial question whether the co-educational institution fosters matrimonial tendencies. This question takes the form, what percentage of the students of either sex who marry have presumably made the acquaintance of their future consorts through the influence of the college associations, or, as expressed in the table, have "married within the college." In view of the opinion so largely prevalent, especially in the early days of coeducation, which led the opponents of that movement to the use of the derogatory term "match factory," it is surprising to find that less than one-fourth of the marrying men (less than one-fifth of all male graduates) married women of the college. In the earlier days the proportion was far less. It is interesting to note that the percentage of men marrying fellow-students steadily increases with each decade. This appears to be accounted for in part by the fact that there is a constantly increasing group of women available for selection. But, as we shall see presently, this conclusion must be drawn with some caution.

Turning our attention to the statistics for the women we meet with a surprising contrast. First, there is the much larger percentage of women than of men who marry fellow-students. The difference is even greater than appears from the returns, for not only are there women who marry and fail to graduate, but also we must remember there was a considerable body of women in the fine arts college, especially in the last two decades, who are excluded from our statistics for the women but, being members of a common social group, marriages with these are accounted in the table for men as "within the college." The explanation most readily offered for this contrast is that the total number of women in the institution is much less than that of the men, hence affording a smaller field of selection for the one sex than for the other. This may be an important factor in the earlier decades and, combined with the small total attendance then, may be a sufficient explanation. But it seems hardly adequate to account for the high percentages in the later decades when the total attendance of women, including the fine arts school, was not only large but equaled or exceeded that of the men. In 1872 there were in the college 26 women and 82 men; in 1882, 129 women and 154 men; in 1892, 321 women and 247 men; and in 1900, 500 women and 506 men.[2]

WOMEN'S MARRIAGES DECREASE

The second surprising feature in this part of the table is the fact that in the last four decades there is a steady decline in the percentages for the women. If the increase of marriage within the college group on the part of the men seemed accounted for by the increased size of the social group and consequent larger field for marriage selection, how shall we account for this precisely reversed result on the part of the women under the same condition? It is not clear that this is at all correlated with the general decline in per cent of marriages, for these last figures are the per cent of married women, not of all women. It may be suggested that while the absolute number in the social group is increasing the ratio of men to women is decreasing, thus rendering the field of selection for the women relatively smaller though absolutely larger. In this case the explanation of the phenomenon is chiefly statistical. Without corresponding data from other co-educational schools further discussion of the matter would seem to be profitless.

We now come to the last six columns of the tables which have to do specifically with the fecundity of the graduates and survival of offspring. Children were accounted as surviving unless known to have died under the age of twenty. This age was selected as approximating independence of parental care. Since there is no uniform practice as to what constitutes "survival," comparison on this point with the findings of others is impracticable. In the original tables the proportion of the sexes in the

[2] Annual Catalogue, Syracuse University.

offspring was determined, but as there appeared to be nothing of significance in the results they are not reproduced here. It is not necessary to enter into further discussion of the details of this part of the tables as the figures are sufficiently clear. By whatever method the facts are measured it is evident that for both sexes there is a steady decline in fecundity from the earlier to the later years. This is in strict conformity with the findings of others as to other institutions, coeducational and non-coeducational, for men or for women, and has been shown to be true also of non-college populations.[3] There appears no reason to believe that this decline is induced by any influence within the college. The factor or factors are more broadly social and the college, any college, is only a phase of the larger problem. It is, however, to be noted from the tables that the married college women under precisely the same educational conditions as the men are reproducing in a distinctly less degree, and this, combined with the lower marriage rate of the last decades, gives a total reproductive rate for all the women graduates of only about half that for the men. It seems conclusive that college-bred women under the same environmental influences are much less reproductive than college-bred men, and by inference are much less reproductive than non-college-bred women of the same social rank, *i.e.*, the wives of college men; for since some college men marry college graduates the task of maintaining the higher average for the men falls chiefly on the non-graduate wives.

INFLUENCE OF COEDUCATION

In view of the facts presented it seems highly probable that Johnson and Stutzmann[4] have erred in their explanation of the low birth rate revealed by their studies of Wellesley College. The conditions at Syracuse seem to have provided nearly everything which these authors found lacking at Wellesley and the figures for the two institutions conform with most surprising closeness. The data for Wellesley are for the classes 1879–1888. The period in our tables most nearly approximating this is the decade 1882–1891. To show the remarkable conformity we reproduce them.

	Wellesley	*Syracuse*
No. of children per graduate	.86	.88
No. of children per married graduate	1.56	1.60

We do not, however, lay great stress upon the closeness of these figures, which are doubtless in some degree a coincidence, but our whole table clearly shows that there prevails at Syracuse the same low birth rate that was found at Wellesley. The results suggest very strongly that we have to deal here with a cause that is not peculiar to this or that college but is in fact very general. Like the decline in birth rate already noted it perhaps pertains to a social group of which the college life is only a phase. Nevertheless, the fact that the college woman in the same educational environment displays such a decidedly and persistently lower reproductive tendency than her brother suggests that there is some special sex reaction to the college environment. Is it not probable that the college curriculum of the past as presented to the women, whether in the coeducational or separate college, has had the effect of segregating from the general population on the average the non-reproductive type of woman? In other words the college environment, whether social or intellectual, whether in its ideals or its discipline, has not so much perverted or suppressed the distinctively female instincts as it has failed sufficiently to appeal to them. As a consequence the women who enter upon the regular college course and carry it to completion are on the average—for there are many exceptions—more or

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[3] Smith, Mary Roberts. Statistics of College and Non-college Women. American Statistical Association Publications, 7: 1.

Engelmann, George J. Education not the Cause of Race Decline. *Popular Science Monthly*, June, 1903.

[4] Johnson, Roswell H., and Stutzmann, Bertha J. Wellesley's Birth Rate. JOURNAL OF HEREDITY, 6: 250–253, 1915.

less lacking in the normal sex instincts. The college has been the means of selecting from the general population the less normal type. This conclusion seems to be confirmed by the discovery of Johnson and Stutzmann that Wellesley women who do not graduate have a higher birth rate than those who do, that is, they approach more nearly to the norm, while those who attain to the highest intellectual honors, Phi Beta Kappa, Durant and Wellesley scholarships, yield the lowest birth rate or are farthest from the norm. Professor Cattell, as cited by those authors, finds also that the wives of American men of science are on the average prolific in reciprocal proportion to the degree of their college attainments. We regret that the Syracuse records did not furnish data for further evidence on this point.

NO CAUSE FOR ALARM

If our reasoning is correct, are we not unduly alarmed at the eugenic disaster which seems to threaten from the low birth rate of this supposedly superior class of women? It is doubtful if they are a superior class except in a strictly limited sense—often a purely intellectual superiority. In reality they represent a highly specialized class of low fecundity, a severely selected type, as Johnson has pointed out, but not well selected for the foundation of a great racial stock from a eugenic standpoint. They are of great value to society in their way and deserving of having their fine qualities developed to the utmost and utilized in the needs of society. For many of them, doubtless, the college courses heretofore offered are well adapted and have been the means of bringing to fruition the socially valuable qualities which they possessed. It is not to be supposed that a different type of college training would have been desirable for them, nor is it evident that any other form of education would have increased their reproductiveness materially. On the contrary, many would have become restless under the system and would have sought relief in some atmosphere that appealed more to their purely intellectual aspirations. But the college should also provide for the needs of their sisters whose domestic and motherly instincts seek equally if less obtrusively the opportunity for full development and expression. The result would not be to increase the reproductive qualities of that type of woman which the higher education has heretofore cherished, but would attract to a higher education the type of woman which is naturally more reproductive. These normal, "all-round," "red-blooded" women are the really superior type and the college should provide a course of training attractive to their instincts and intended to develop all their innate powers and capacities to the highest efficiency.

Since this paper was ready for the press the marriage rates for coeducational institutions recently published by the editor of the JOURNAL[5] have come to my attention and seem to give some additional support to this view. For the institutions yielding the highest marriage rates are state schools that make much of courses in applied science adapted to the interests of home builders and social efficiency. Syracuse and Stanford, more closely confined to the classics, humanities, and pure science, present figures so nearly identical for the same period as to be, the editor remarks in a private letter, "uncanny."

There remains for discussion the comparison of our tables with similar tables compiled for other institutions such as the work of Dr. John C. Phillips on Harvard and Yale students[6] and Prof. Robert J. Sprague's figures for

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[5] Stanford's Marriage Rate. JOURNAL OF HEREDITY, viii, pp. 170–173, April, 1917. See also Coeducation and Marriage. JOURNAL OF HEREDITY, viii, pp. 43–45, January, 1917. Stanford and Syracuse are at opposite sides of the continent; the marriage rate of their graduates for the last decade of the nineteenth century is as follows:

	Men	*Women*
Stanford	73.2%	48.5%
Syracuse	72.7	48.6

[6] Phillips, John C. *Op. cit.*

TABLE I.—*Women Graduates of Syracuse University*

Decades	Average number of graduates per class	Average number married per class	Per cent of graduates married	Average age at marriage	Average number marrying within college per class	Per cent of married marrying within college	Per cent of married childless	Per cent of graduates having 2 or more children	Average number of children		Average number of children surviving	
									per married	per graduates	per married	per graduates
'52–'61	1.5	1.3	87	25.8	.5	38	8	60	2.31	2	2	1.73
'62–'71	3.1	2.7	87	26.4	1.7	65	11	59	2.26	1.97	1.93	1.68
'72–'81	3.6	2.9	81	30.9	1.5	52	31	34	1.62	1.31	1.31	1.06
'82–'91	6.9	3.8	55	27.8	1.7	45	26	50	1.60	.88	1.45	.79
'92–'01	25.1	12.2	48	27.6	4.9	40	34	34	1.12	.54	1.07	.52
Totals	8.04	4.58	57	27.7	2.06	45	28	42	1.46	.83	1.31	.75

TABLE II.—*Men Graduates of Syracuse University*

Decades	Average number of graduates per class	Average number married per class	Per cent of graduates married	Average age at marriage	Average number marrying within college per class	Per cent of married marrying within college	Per cent of married childless	Per cent of graduates having 2 or more children	Average number of children		Average number of children surviving	
									per married	per graduates	per married	per graduates
'52–'61	6.8	5.5	81	28.2	.7	13	5	63	3.29	2.66	2.62	2.12
'62–'71	9.1	7.9	87	28.4	1.2	15	14	71	2.51	2.18	1.95	1.69
'72–'81	16.4	14.8	90	29.1	2.7	18	14	55	2.30	2.08	1.96	1.77
'82–'91	22.4	18.9	84	29.5	4.4	23	21	50	2.17	1.83	2.04	1.72
'92–'01	36.6	26.6	73	28.9	8.3	31	27	31	1.46	1.06	1.38	1
Totals	18.3	14.7	81	28.8	3.46	24	20	45	2.06	1.66	1.82	1.47

the women's colleges,[7] etc. These may be disposed of briefly for our results simply confirm the findings of others in all essential facts. The most striking difference to be observed is the much higher percentage of married men at Syracuse than at either Harvard or Yale. At first thought one would say it is the influence of coeducation. But Wesleyan and Amherst, both non-coeducational institutions, are shown by Professor Hall[8] to have each a higher marriage rate for the same periods than even Syracuse. Comparing the women's table with the statistics of women's colleges as reported by Professor Sprague we find only that the marriage and the birth rates of Syracuse women are distinctly lower than those of Mount Holyoke, higher than for Bryn Mawr, a little less than for Vassar, and about the same as at Wellesley. We are disposed to think that these differences, so far as they are sufficiently large to have any significance, are simply indexes of the ulterior social group to

[7] Sprague, Robert J. Education and Race Suicide. JOURNAL OF HEREDITY, 6: 158–162. 1915.

[8] Hall, G. Stanley, and Smith, Theodate L. Marriage and Fecundity of College Men and Women. *Pedagogical Seminary*, 10: 275–314. 1903.

which the student body pertains. The factor of coeducation appears to have produced no specific influence, nor is there clear evidence that the college environment has materially affected the results. The problem is to a considerable degree one of inherent character of the women, in which the college has served chiefly as a selective agent for a specific type.

The Problem of Handedness in Education

Approaching the problem of left-handedness from the psychological side, Prof. W. F. Jones, of the University of South Dakota, described his researches at the last meeting of the American Psychological Association.

Out of 10,000 persons 417 are born left handed, 9,853 are born right handed; 4% of the race are lefthanded, 96% are right handed. Out of 417 born left-handers, 323 shift to the right hand. Seventy-seven per cent of born left-handers adopt the minor arm. Out of 417 born left handed, 4 are shifted by accident, 1% of all lefthanders; 319 are shifted by purposive interference; 94 are allowed to use the major arm. Out of 9,583 born righthanders 96 are shifted to the left hand, 1% (accident). Four hundred and nineteen persons (323 plus 96) out of 10,000 adopt the wrong arm, that is, one person out of twenty-five is using the minor arm.

Conclusion from skill tests of the three types of handedness are: (1) The pure lefthander reveals no less skill than the pure righthander; (2) the shiftover is regularly deficient in hand and arm skill; though the average skill of his two hands is equal to the average skill of the two hands of the right or lefthander, he has two minor hands and arms rather than one dextral and one minor; (3) it is possible to shift back to the major arm if the shiftover does not show a muscle swell of minor arm exceeding that of the major (born) arm, and if the shiftover is below adolescence the backshift should be made. His work agrees in general with that of other students.

The Offspring of Marriages of the Deaf

GRAPHICAL STUDIES OF MARRIAGES OF THE DEAF IN AMERICA, by Alexander Graham Bell, with an introduction by Fred DeLand. Pp. 300. Washington, D. C.: The Volta Bureau, 1917.

In his book, "Marriages of the Deaf in America," published in 1898, E. A. Fay recorded data about 2,644 marriages where children had been produced, and where one or more of the parents was deaf. Dr. Bell has made a graphical representation of each of these cases, and pedigree charts of the 300 cases in which there were deaf offspring. The dysgenic effect of the marriage of deaf persons can therefore be seen at a glance. It is found that the average number of children is 3.48, and that 56% of them are deaf. This, however, refers only to marriages which resulted in at least one deaf child. Most of the marriages, in which at least one of the parents was deaf, did not result in deaf offspring. Of the total number of children (6,782) from all marriages, only 588 or 8.6% were deaf.

A Horseman's Views on Eugenics

"The Right To Be Well Born" is the title of a book lately published by W. E. D. Stokes, president of the Patchen Wilkes Stock Farm, Lexington, Ky. Mr. Stokes is one of the best-known breeders of thoroughbred horses in the United States, and believes that many of the methods which have been successful in that industry could be profitably applied to the human race. His book is one of the most original and thought-provoking of recent contributions to the literature of eugenics and should have a stimulating influence.

HIDDEN FEEBLEMINDEDNESS

One Person in Fourteen of the American Population Probably Carries the Trait in a Recessive Form, Although Normal to all Appearances—One-Fourth of Offspring will be Feebleminded if Mating is Made with Another Carrier

E. M. East
Bussey Institution, Forest Hills, Mass.

THE increase in the number of feebleminded in the United States during the past few years has been such that the heredity of the trait, and the classification and treatment of those so afflicted, have been the subject of much careful study. The result of this activity has been very creditable. Thanks to the researches of Goddard, the method of inheritance of feeblemindedness is as clear as that of any other heritable variation in the human race. Owing to the ingenious psychological methods of Binet and Simon, the grade of mentality can be determined reasonably well. Even our slowly moving legislative bodies have been somewhat disturbed by the facts and have passed a considerable number of laws designed to cut off this defective germplasm, either through segregation of the sexes during the reproductive period or by sterilization.

One can have only words of commendation for the serious efforts to face the problem; nevertheless, in the numerous papers on feeblemindedness that have been published during the last decade, not a single author appears to have appreciated the real menace. Our modern Red Cross Knights have glimpsed but the face of the dragon.

Goddard has shown that feeblemindedness is transmitted as a Mendelian recessive. In other words feebleminded individuals may be produced in three ways. If feebleminded mates with feebleminded all of the offspring will be feebleminded. If a feebleminded individual mates with one carrying the trait in his or her germcells, on the average one-half of the offspring will be feebleminded. It is these two types that segregation or sterilization will affect. But these are not the only sources of feeblemindedness, and perhaps they are not the most dangerous. If two carriers of feeblemindedness mate, one-quarter of their offspring will exhibit the trait and one-half of them will transmit it. Let us endeavor to see what this means.

THE NUMBER AFFECTED

It appears that in our present population of 100,000,000 or thereabouts, there are 300,000 persons who are feebleminded through an hereditary defect, a ratio of 3 per 1,000. This is an estimate to be sure, but it is so conservative that it probably veils the true state of affairs.

Now how many of these defectives have been the result of a mating wherein at least one of the parents was feebleminded? This question is a difficult one and can only be answered with a rough approximation. The best estimate that I can make from a careful examination of the meagre statistics at present available is 100,000. The dose must not be too bitter, however, so let us double this estimate. This leaves 100,000 feebleminded persons that must have been produced by the mating of two transmitters of feeblemindedness who did not show defective mentality themselves, unless an unprecedented percentage of origin *de novo* be assumed.

These 100,000 defectives were produced during a period in which there were rather less than 20,000,000 married couples of reproductive age. They were produced by parents both of which carried feeblemindedness. But only

one-fourth of the progeny of such matings show feeblemindedness. Therefore, at least 100,000 couples of this type were reproducing during this generation. This would presuppose the survival of four children per couple long enough to have their mental status determined, an assumption that would probably require a total reproductivity of seven children per married pair. Among the children from these matings would be some 200,000 carriers of defective germ-cells, but we will omit them from our considerations. The important point is that out of 20,000,000 pairs of married persons, if we treat the problem as static, 100,000 were transmitting feeblemindedness. What then is the number of such persons in the population?

Let us state the question in another way. A certain number of persons out of a population of 40,000,000 of a marriageable age have defective germ-cells. If two of them marry, one-quarter of their children will be feebleminded. If 100,000 of such marriages did occur, what is the ratio of carriers of feeblemindedness to normals in the general population? The correct answer will depend of course upon how much selective mating takes place. There is unquestionably a general tendency for carriers of feeblemindedness to be brought together and a marriage to result. But this cannot be taken into account very accurately and had best be left out of our calculations.

Pairing among carriers of feeblemindedness has occurred in the ratio of 1 to 200 marriages; then, if no selective mating has taken place, carriers of feeblemindedness must occur in the general population in the ratio of 1 to 14.

One-fourteenth is approximately the square root of 1/200. If 1/14 of the population carry feeblemindedness and 13/14 are normal, then the probability of normal mating with normal is $13/14 \times 13/14 = 169/196$, the probability of normal mating with carriers of feeblemindedness is $1/14 \times 13/14 + 13/14 \times 1/14 = 26/196$, and the probability of two carriers of feeblemindedness mating is $1/14 \times 1/14 = 1/196$.

Possibly this figure is somewhat too high for the single trait feeblemindedness. We have not corrected for changes in the population during the length of the period considered or for selective mating. But, to balance this we have used a low estimate of the number of feebleminded, a high estimate of the number of defectives produced by parents of which at least one exhibited defects, and a high birth-rate in families of those transmitting the defect. Further, no mention has been made of epilepsy and of certain types of insanity, which are inherited in the same way, and to which the same line of reasoning applies. In view of these facts it is probable that the conclusion that 1 person out of every 14 carries the basis of serious mental defectiveness in one-half of his or her reproductive cells understates rather than overstates the facts.

The problem of cutting off defective germ-plasm, therefore, is not the comparatively simple one of preventing the multiplication of those so affected. This task, though sufficiently difficult in practice, is possible: the way has been pointed out; something has been accomplished. It is rather the almost hopeless task of reducing the birth-rate among transmitters of serious defects.

NEED FOR RESEARCH

A stupendous task necessitates prodigious efforts. Already there is a tremendous selective birth-rate in favor of lesser civic worth, and it is extremely doubtful whether, under our present economic system, much can be accomplished by recommending early marriages and large families among those whose accomplishments have proved their social value. Whether family limitation among those carrying defective germ-plasms can be effected must be decided in the future. It will be a distant future if a stupid government persists in refusing to countenance rational parenthood among those least fitted to reproduce the race, the while shutting one eye and winking the other at what has become a national practice among those best fitted to build a

greater America. There is one suggestion, however, at which no one will cavil. We have assumed that a normal mentality is completely dominant over a defective one. Is this true? Complete dominance is rare among those characters commonly studied by animal and plant geneticists. Is it not likely that the Binet-Simon or other proper tests would show that carriers of mental defects exhibit a lower mentality than pure normals? Would it not be wise to start some investigations along this line?

Marriage Rate of Iowa State College Women

In the JOURNAL OF HEREDITY for January, 1917, are brought together figures of several western co-educational colleges, showing the proportion of married women graduates in comparison with certain eastern women's colleges. The figures here added are for Iowa State College, as taken from the Alumni Directory issued June, 1916. During the period from 1872 to 1905, inclusive, 315 women graduated, and 229 of these, or 72.7%, married. During the five-year period 1900–1904, 39 out of the 56 women graduates married, or 69.6%. For both periods, the figures are higher than for any other college given. Earlier and later periods compared as follows:

Period	*Per cent married*
1872–81	95.8
1882–91	62.5
1892–01	71.2
1902–06	69.0

The decline is not regular, as for some reason the second decade shows the lowest record. But even this is high compared with eastern figures. The rather remarkable fact appears from the record of the first nine classes that graduated, from 1872 to 1879, and also that of the class of 1885, that all of the forty-eight women graduates of these ten early classes married.

J. C. BLUMER, *Tucson, Ariz.*

The Lethal Factor in Yellow Mice

Yellow mice are familiar to fanciers, but none has been found which breeds true. This has been explained by the assumption that all living yellow mice have received their color from only one parent. If a mouse receives yellow from both parents, it is supposed, he receives necessarily, at the same time, a lethal factor which prevents development of the embryo; or technically, the homozygous zygotes which should theoretically exist are for some reason not viable. All breeding facts bear out this hypothesis, nor is this the only known case where a lethal factor seems to be inherited, which prevents the development of all individuals with a certain genetic constitution. But it has been desirable to have embryological evidence, and Prof. W. B. Kirkham, of Yale, reported on it at the last meeting of the American Society of Zoölogists. He found that many degenerated embryos resulted from every mating of yellow mice, but only a few when other colors were mated. The hypothesis that a double dose of yellow coat-color means death for the embryo that receives it, is therefore substantiated to some extent.

The Cost of Defectives to the Nation

The annual cost of the socially inadequate in the United States is approximately $100,000,000, according to the Eugenics Record Office, which has recently completed a survey of the subject. The States pay out every year $73,000,000 for the support of their defectives, degenerates and delinquents, and the counties, municipalities and private institutions account for the other $27,000,000. This hundred million dollars of annual expense represents a part of the price paid for lack of eugenics; but it is only the direct price. The indirect one is much larger. Details will be published by the Census Bureau.

A BUD VARIATION OF EUONYMUS

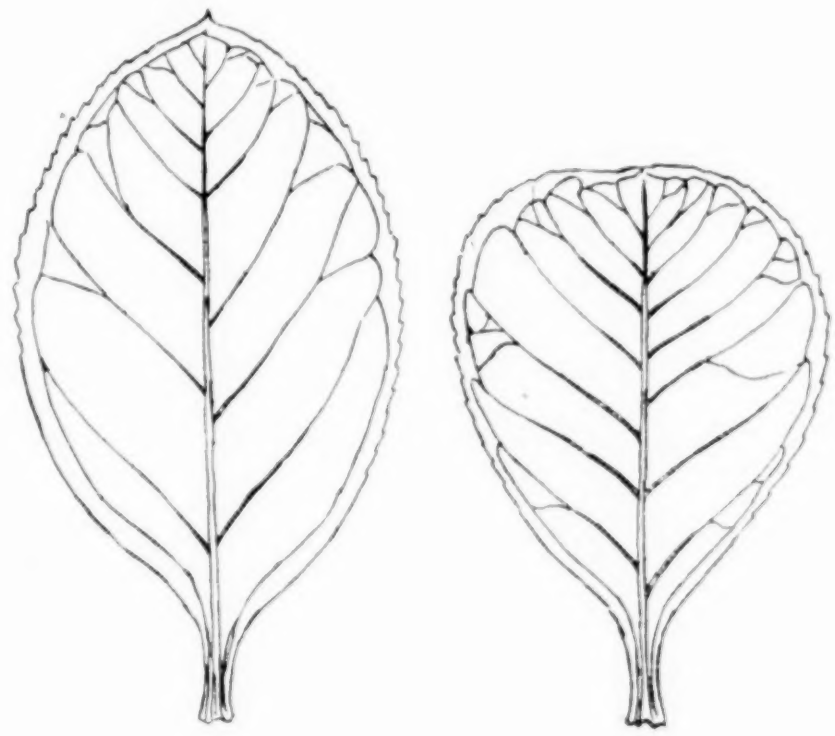
A. D. SHAMEL, *Riverside, Cal.*

THE accompanying photograph (Fig. 5), shows a small limb of *Euonymus japonicus*, an evergreen shrub, belonging to the family Celastraceae.[1] The leaves of this species are normally rounded ovate. The margins of the leaves are toothed. The color of the foliage is a deep green. The small pale green flowers are composed of four petals, are usually borne two to five together on a stalk in the axils of the leaves, and are succeeded by top-shaped seed-vessels of three blunt lobes, and as many cells, each containing a solitary seed. In Southern California during the winter months these fruits become more conspicuous among the leaves by assuming a pink color which makes them highly ornamental. The lobes of the capsule, finally assuming a bright rose color, open at a projecting angle and disclose the seed wrapped in an orange-colored arillus. The foliage, flowers, and fruit are said to be poisonous, but the fruits are sometimes used as a dye. The wood, which is of a light yellow hue, being strong, compact, and easily worked is applied in some countries to many useful purposes; *e. g.* skewers, pegs for shoes, spindles, etc. The charcoal made from the young shoots is used by artists on account of its smoothness and ease with which it is erased.

In Southern California this shrub is highly prized and commonly used for ornamental plantings, sometimes for hedges and otherwise for individual shrubs. Eight or more varieties of this species are propagated commercially by California nurserymen. Of these *E. japonicus argenteo-variegatus* (Silver variegated Euonymus) is the one most commonly found in the gardens and other ornamental plantings in the vicinity of Riverside. This variety, on account of its variegated foliage, the silver-like margins and irregular stripes of the leaves, is very striking in appearance even from a considerable distance. The shrubs have an upright habit of growth. It was developed from branch variations of *E. japonicus*, an example of which is shown in the accompanying photograph.

In the variegated form the leaves differ from the ordinary form particularly as regards shape and color. The shape of the ordinary leaf is ovate with an obtuse apex. The shape of the variegated leaf is obovate and the apex is usually truncate or retuse. (See Fig. 6.) The margins of the leaves of the ordinary form are usually serrate, while the serrations of the variegated leaves are much less marked, so much so in some cases as to be almost invisible without very close inspection.

The color of the ordinary leaves is a uniform deep green, slightly deeper in shade on the upper than on the under



CHANGE IN LEAF FORM

At the left is the ordinary leaf of Euonymus, at the right the leaf of the variegated form. It is evident that the same bud variation which produces the change in color, also produces changes in numerous other features. (Fig. 6.)

[1] The Treasury of Botany, part I, p. 475.

THE ORIGIN OF A VARIETY OF EUONYMUS

On this green shrub, part of a branch has become variegated, due to some internal change which has affected the pigment. But internal changes of this sort are apparently never confined to a single character. Not only is the color of the leaves changed, but their shape is likewise altered, and the difference in appearance extends to the stem. Changes of this sort are rather common, and probably have not much importance in normal evolution, but they are sometimes of much value to gardeners, many ornamental varieties of plants having originated in the same way that the silver-variegated Euonymus did. (Fig. 5.)

sides. The color of the variegated leaves is very light green, very different from the color of the ordinary leaves, so much so in fact that it can be easily distinguished by even the most casual observer. The variegated leaves usually have a narrow margin of white or silver color around or nearly around the entire leaf. Irregular areas or stripes of white or silver color usually mark the upper surface of the remainder of the variegated leaf area, while the under surface is usually of a more uniform color.

The stems of the variegated branches are of a silver color in contrast with the uniform green of the ordinary stems.

I have found green branches frequently occurring in variegated shrubs, and variegated branches in green shrubs. A propagator of Riverside informs me that he has repeatedly propagated both varieties from bud variations through the selection of cuttings. In this way, he has isolated the variegated form from the green one, and the green form from the variegated.

This case is presented as an instance of the origin of a valuable cultivated variety of plants through the propagation of bud variations. It is probable that some of the other varieties, if not all, of *E. japonicus* have been developed from bud variations.

It is also a good illustration of the fact that a bud variation rarely affects one character of the plant alone; it frequently produces changes in many different characters simultaneously.

A Valuable Text-Book of Animal Breeding

THE BREEDING OF ANIMALS, by F. B. Mumford, dean of the college of agriculture and director of the experiment station of the University of Missouri. Pp. 310, price $1.75. New York, The Macmillan Co., 66 Fifth Avenue, 1917. (Rural Text-book Series, L. H. Bailey, Editor.)

Most of the questions which a live-stock breeder asks are answered in Dean Mumford's book, which can be cordially recommended. Reproduction, inheritance, and development all receive full discussion, illustrated with numerous examples, and with the omission of most of the unnecessary technicalities. Of course, neither this book nor any other will teach a man how to become a successful breeder; that art can be learned only by practice. Professor Mumford's chapter on "The Practice of Breeding" is perhaps not quite up to the standard o' the rest of the book, but it is really difficult to say anything on that subject, which will be of value for immediate application. On the whole, however, his book gives the facts which the breeder, whether a novice or an old hand, wants to know, and it is marked by sound judgment. The errors noticed are few and of minor importance.

Families of American Men of Science

Ten per cent of the well-known American men of science are unmarried, according to J. McKenn Cattell, who has studied the histories of 1,000 of them (*The Scientific Monthly*, March, 1917). Considering their ages, a scientific man is more likely to be married than a man taken at random from the community. At the average age of 29.5 years, they married wives aged on the average, 26 6 years. The American men of science have on the average seven-tenths of an adult son, each. Family limitation is much practised.

The Number of Chromosomes in Man

The exact number of chromosomes in the germ-cells of man has long been in doubt. H. L. Wieman of the University of Cincinnati reports, in the *American Journal of Anatomy* (January, 1917), a study which convinces him that the reduced number is twelve, one of which is the sex-chromosome. The number is the same in both negro and white races, he finds—previous work had led to the belief that the negro had twice as many as the white.

THE SWEATING APPARATUS

Tropical Races Are Provided with More Sweat Glands Than Are the White Races of Northern Climates—Valuable Adaption Brought About by Evolution

IN THE course of evolution the races of the tropics must have become different from the northern races in many ways. Skin color is the most conspicuous one. Differences in disease resistance are of great importance. It has further been suggested that the tropical peoples have a more effective mechanism for regulating the internal heat of the body than have the residents of cooler climes.

The body temperature is partly kept down through the evaporation of sweat from its surface, and it has been said that the sweat glands of the tropical races are larger and more numerous than those of northerners. It has also been alleged that they work in a different way: "According to Aron, the Negrito secretes small beads of sweat over the entire body, which soon forms a thin film. As the whole surface of the body is covered by this water film, the maximum cooling effect from evaporation is attained. In the case of the white man, on the other hand, the sweating is practically limited to certain areas of the body surface. In these areas the sweating may be quite profuse, but as most of it drops off, comparatively little cooling effect from evaporation is produced."

When American men of science became established in the Philippines, one of the investigations they undertook was to get more definite evidence about the differences in adaptation of various races to life in the tropics. This is not merely a matter of academic interest; if certain adaptations are necessary to enable a race to live in the tropics, and if the white race lacks these adaptations, it is evident that tropical colonization by the white race will never be permanent. But if there are no unchangeable differences of this sort; if it is merely a question of proper clothing and diet and knowing how to care for the health, the white races might be able to spread over a great deal of fertile territory outside of the temperate zone.

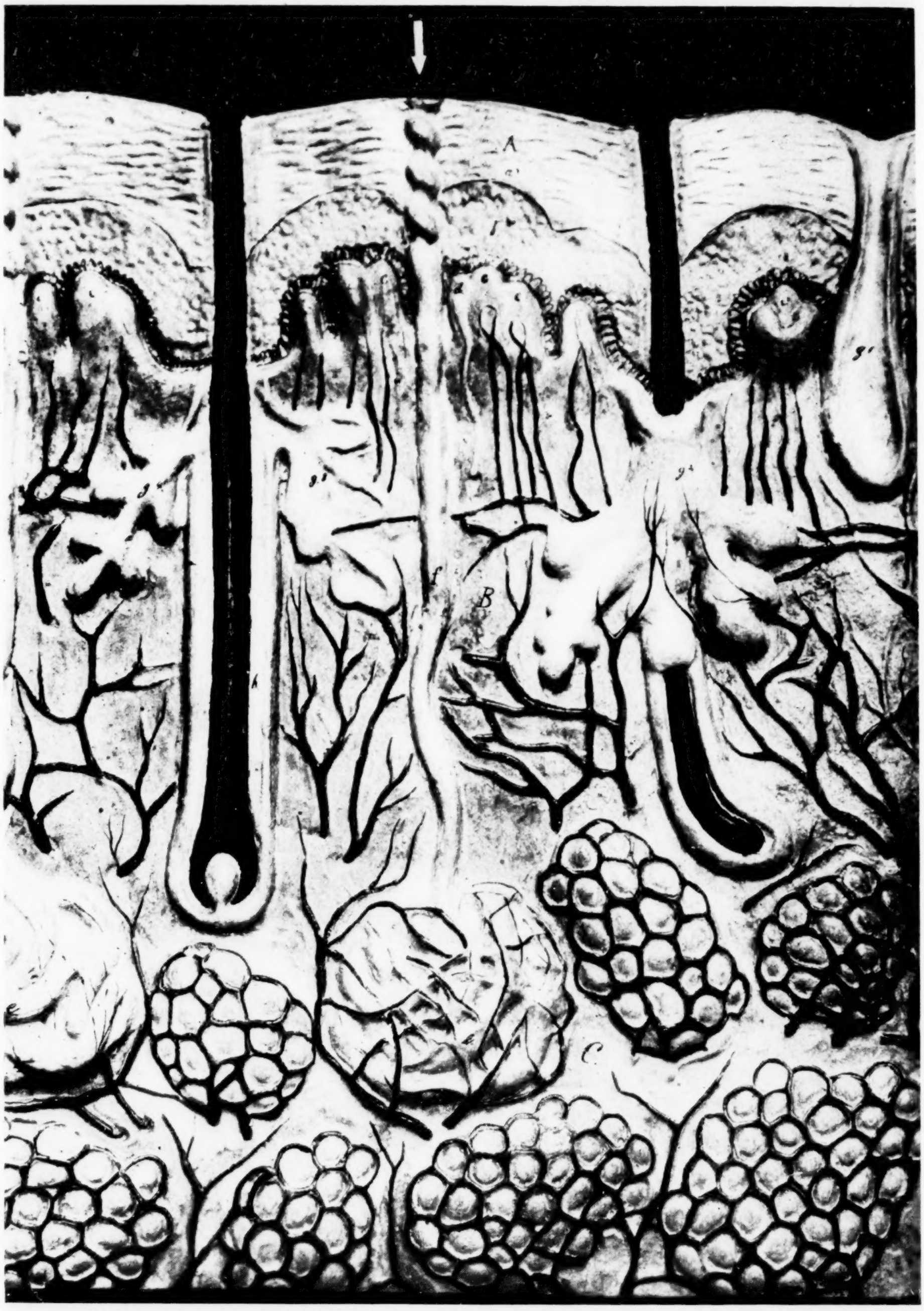
The late Lieut. Col. Chas. E. Woodruff brought together a great deal of evidence to show that the light skin of the white race is an almost fatal handicap in warm climates. The Philippine students proposed to investigate as many similar characters as possible, and Clark and Lhamon undertook the study of sweat glands. They have recently published a preliminary report[1] which shows that the alleged differences do exist, and that they are of considerable extent.

A count of more than a quarter of a million sweat glands in individuals of different races has shown them that there is much variation in size in an individual. Those on the palm of the hand and the sole of the foot are the most constant in size, and also appear first in the embryo. It seems probable that the glands on those two surfaces are more useful to moisten the skin and prevent slipping than they are to reduce body temperature.

The following table shows the average number of glands per square centimeter of skin area on the fingers of men of various races:

American (white)	558
American (negro)	597
Filipino	653
Moro	684
Negrito (adult)	709
Hindu (Sikh?)	738
Negrito (youth)	950

[1] Observations on the sweat glands of tropical and northern races. By Elbert Clark and Rushkin H. Lhamon, Department of Anatomy, University of Chicago, *Anat. Rec.*, xii, pp. 139–149, February, 1917.



AN IMPORTANT PART OF THE BODY'S REFRIGERATING APPARATUS

Among other functions, the sweat glands allow water to evaporate from the surface of the body, thereby reducing its temperature in warm weather. The above model shows two conspicuous black hairs and between them (its mouth marked by an arrow at the top of the picture) a sweat gland. From its opening on the surface, a fine tube which may be as much as a third of an inch long runs down and ends in a coil, surrounded by capillary blood vessels. Water from the blood filters through the walls of these vessels into the sweat gland and is discharged on the surface of the body. The tropical races, who have most need to keep the body cool, are provided with many more sweat glands than are the northern peoples—an example of their constitutional adaptation, through evolution, to the climate in which they live. Photograph from René Bache. (Fig. 7.)

"Taking the American white soldier as the standard, the number of sweat glands per unit of skin area was found to be 6.83% greater in the American negro soldier, 16.61% greater in the Filipino soldier, 23.34% greater in the Moro soldier, 26.81% greater in the adult Negritos, 31.72% greater in the Hindu, and 69.82% greater in the Negrito youths and children. The greater number of sweat glands per unit area with the Negrito youth and child is no doubt due to a corresponding difference in size of individuals. As all the sweat glands are fully formed at birth it is merely a question of the increase in skin area during growth bringing about a dispersion of the glands."

Thus the supposition that evolution has, by natural selection, provided tropical races with more sweat glands than the northern races, is borne out by the actual counts. The writers conclude:

"We are not able to confirm Aron's observation that the tropical aborigines secrete only small beads of sweat over the entire body. On two tramping expeditions in the mountains of the Philippines which we were fortunate enough to arrange with a number of Negritos we observed streams of sweat running down the back, and copious sweating on scalp, forehead and face and sweat dripping from the chin."

Research in Plant Genetics

Among the genetics problems under investigation by A. F. Blakeslee at the Carnegie Institution Laboratory, Cold Spring Harbor, L. I. (says the annual report of the institution) are: inheritance of self-sterility in Rudbeckia, Helianthus, and Verbena, parthenocarpy in cucumbers, chemical and physical differences between the sexes in dioecious plants, the annual habit in beets, various characters in Geodetia, Clarkia, Portulaca, Fraxinus, Betula, Morus, Populus, and Salix," and particularly the inheritance of mutations in *Rudbeckia hirta* (15,000 pedigreed plants were grown last year) and Datura.

A New Handbook of Mendelism

A MANUAL OF MENDELISM, by James Wilson, Professor of Agriculture in the Royal College of Science for Ireland, Dublin. Pp. 152. London: A. & C. Black, Ltd., 1916.

Professor Wilson first gives a historical review of Mendelism and a description of its fundamental principles, and then in a comprehensive and well-planned way outlines the additions and extensions which he thinks justified. The book is well written, but some of the most important points are unfortunately supported by evidence, particularly from animal breeding, which seems to the reviewer to be of more than doubtful validity.

A Posthumous Book by Darbishire

AN INTRODUCTION TO A BIOLOGY, and other papers, by A. D. Darbishire. Pp. 291, price $2.50 net. Funk & Wagnalls Co. 360 Fourth Avenue, New York, 1917.

Mr. Darbishire died recently while training for military service in England, and most of his published papers on genetics have been collected in this posthumous volume. The first eighty-eight pages are taken up by the essay which gives the book its title, and which represents the unfinished attempt of the author to interpret the vitalistic biology of Samuel Butler and Henri Bergson. It is agreeably written and stimulating of thought, but unfortunately the part which the author had completed was only introductory, and therefore is suggestive rather than convincing. The other papers deal principally with the supposed conflict between Mendelism and biometry, and are already known to geneticists. While they possess real value, the longest of them are considerably out of date. On the whole, the book is not so much a contribution to science as a self-revelation of the frank, idealistic, enthusiastic author, for whom the reader can hardly help carrying away the feeling of warm friendship which it is said was experienced by all who met him during his lifetime.

COLOR INHERITANCE IN MAMMALS

Results of Experimental Breeding Can Be Linked up With Chemical Researches on Pigments—Coat Colors of All Mammals Classified as Due to Variations in Action of Two Enzymes

SEWALL WRIGHT
Bureau of Animal Industry, Washington, D. C.

HEREDITY as looked upon since the time of Weismann is relatively simple to understand. It consists merely in the persistence of a certain cell constitution (in the germ cells) through an unending succession of cell divisions. We see something of the mechanism, back of this persistence, in mitosis. We understand complications brought about by the reduction division and by the union of two germ cells at fertilization. Thus we no longer puzzle over the problem as to how an individual packs his characters into his reproductive cells, the problem which led to Darwin's theory of pangenesis. But if heredity seems simpler than it did half a century ago, the problem of development has become more complex. We see clearly that development is no mere unfolding and growth of elements already present in the fertilized egg or even a sorting out of germinal rudiments for parts of the organism. The germ cell has a certain highly complex constitution, the adult organism another such constitution, and between the two is no simple one-to-one relationship. An almost infinitely complex series of interactions of elements must take place at each stage of development. The difficulty in the study of heredity is that the characters of the germ cell must be deduced from a study of variation in characters at the other end of the developmental history. The wonder is that with such a method it has been possible at all to demonstrate unit variations in the germ cell. One of the most remarkable results of recent genetic work has been the detailed correlation of these hypothetical characters of the germ cell with structures actually observed there.

It remains for genetics to assist embryology and biochemistry in filling in the links in the chain between germ cell and adult in specific cases. Variations of adult characters must be traced back through the contributing causes at each stage of development until, if possible, something is learned of the nature of the ultimate germinal factors involved and, on the other hand, the ramifying influences of unit variations in the germ cell must be traced forward through development. Probably the most favorable point of attack for such work is in color inheritance in animals and plants. A larger number of unit factors have been isolated than in other kinds of characters and are available for comparative study. Much progress has been made in the chemistry and mode of formation of many of the pigments, notably the melanins, with which we are chiefly concerned in the higher animals. The very fact that it has been relatively easy to isolate unit factors in work on color inheritance suggests that in this case the chain of processes between germ cell and adult may be relatively simple. Observations which indicate that melanin pigment is formed in the cytoplasm of cells by the secretion of oxidizing enzymes from the nucleus suggest that the chain may be very short indeed when it is remembered that genetic factors are probably characters of the chromosomes and that these seem to be distributed unchanged from the germ cell to all other cells.

The present paper is an attempt to make as simple a classification of color factors in mammals, based on their effects, as possible, and to suggest a working hypothesis which will relate the biochemical knowledge concerning melanism with this classification and

with certain peculiar relations between the colors. The writer wishes to emphasize, however, that for the present the chemical terms are used rather for the sake of giving a definite scheme to which genetic facts may be referred than for their own sake. Since the earliest work on color inheritance, many geneticists, notably Cuénot,[1] Castle,[2] and Little,[3] have tried to give a physiological interpretation to their results. The hypothesis advanced here is based to some extent on their conclusions with modifications intended to bring under one point of view certain curious new facts.

COLOR IN MAMMALS

Melanin pigment is found in the skin, fur and eyes of mammals. The present paper will deal largely with the gross effects as our knowledge of the ultimate differences of the colors is still very unsatisfactory. Only mammals are dealt with, as in other classes on which genetic work has been done the pigment colors are largely masked by structural effects.

The most highly pigmented condition is found in the color black. The pigment granules in this case are not really black but a very dark sepia brown. White in mammals seems always to be a structural color found in the absence of all pigment. There are two distinct series by which black may be reduced toward white. There is first the type of dilution found in brown and tow-colored human hair, or in dilute black guinea-pigs, which reveals the sepia color of the pigment. A very different kind of dilution of black is to be seen in the so-called blue or maltese mammals—blue mice and rabbits, maltese cats, etc. The effect is somewhat similar to that in blue roans among horses and cattle and seems to be due to a similar cause on a finer scale. Blue roans have an intermingling of jet black hairs and white hairs while the maltese mammals have dense black pigment masses alternating with colorless spaces within the hair.

The colors which do not enter into either of these dilution series or their combinations are those which have a distinct orange-yellow tinge such as is seen conspicuously in red human hair, red and yellow cattle, bay, chestnut and dun horses, tan dogs, etc. The most highly pigmented colors of this kind are the so-called reds. The pigment granules appear orange-yellow in such hair, but it does not seem to be settled whether there is an essential chemical difference from sepia-brown granules or merely some structural difference. The appearance of the intense reds varies somewhat in different mammals, but there seems little reason for doubting their essential similarity. Red undergoes different modes of dilution comparable to those described for black. Reduction to yellow or cream is comparable to the sepia type of dilution of black, while a more coarsely granular type of dilution comparable to maltese is found in light reds. These light reds are slightly redder in hue than the yellows of similar intensity. The two series may, of course, be combined.

Finally there are intergrades of various sorts between the different sepia and yellow series. A coarse-grained mixture gives the effect of bay, dun, or sooty yellow depending on the intensity of the colors. A finer type of intergrade seems to be present in the chocolate color of brown mice, rabbits, guinea-pigs and liver-colored dogs. These browns, however, are much closer to the sepias than to the reds and yellows and are not always distinguishable. Genetic evidence sharply distinguishes browns which are due to reduction of black toward white, and browns which are reductions toward yellow.

By combining the different kinds of dilution with the different kinds of intergrades between sepia and yellow an almost infinite variety of colors is produced, while the complex patterns in which these colors may be distributed make possible still further diversity in color effect.

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[1] Cuénot, L. 1903. *Arch. Zool. Exp. et Gén.* (4), Vol. i. Notes et Revue, p. 33.

[2] Castle, W. E., H. E. Walter, R. C. Mullenix and S. Cobb, 1909. Carn. Inst. Wash. Pub., 114.

[3] Little, C. C., 1913. Carn. Inst. Wash. Pub., 179.

Skin color in general corresponds roughly with hair color. The pigments in the eyes are like those in the skin and fur, but the appearance is generally much modified by structural effects. In dilute human eyes, for example, the appearance is blue, although the pigment is sepia brown. In the rodents the reflection from the back of the retina gives a red color when the pigment is reduced, which in the complete absence of pigment becomes pink as in albinos.

CHEMISTRY OF MELANIN

A large amount of work in the last twenty years has firmly established the hypothesis that melanin is an oxidation product of tyrosin or related products of protein metabolism. Enzymes have been extracted in a great many animals and plants, which have the power of oxidizing tyrosin and related substances to dark brown pigments closely resembling the natural melanins. Studies of Hooker,[4] on cultures in vitro of frog mesenchyme indicate that the pigment granules are formed in the cytoplasm immediately surrounding the nucleus, presumably under the influence of oxidizing enzymes secreted by the latter.

The nature of the differences between colors is still far from clear. Onslow[5] could find no chemical differences between pigments extracted from black and yellow rabbits and considers that they differ merely quantitatively. Most others do find chemical differences as well as physical ones. Black pigment seems always to be granular, while red may be either granular or diffuse. Lloyd-Jones[6] found only granules in both intense and dilute black pigeons, and found red granules in red pigeons, but merely a diffuse yellow in the dilute yellows. The Davenports[7] found granules in brown and black human hair, but merely a diffuse color in auburn hair.

There is a distinct difference in solubility between the dark colors and yellow. Miss Durham[8] found that yellow granules in yellow mice dissolve quickly in potash, brown less quickly, and black not at all. Gortner[9] was able to separate two pigments in black wool—one easily soluble in very dilute alkali and also soluble in dilute acids, while the other dissolved only slowly in alkali and not at all in dilute acids. This, of course, is a chemical difference. The acid-soluble type was of protein nature. He considered it to be a diffuse coloration of the keratin structure, while he identified the insoluble type with the granules. In red human hair he found only the acid-soluble type. In brown horse hair and black wool he found both, while in brown and black human hair, black rabbit hair and black feathers of domestic poultry and crows he found only the insoluble type. His two types evidently correspond more or less closely with yellow and black pigment. This difference in solubility does not necessarily indicate that yellow and black are produced from different chromogens. Indeed, Gortner has shown that the insoluble type may be produced from the soluble by treatment with strong alkali. In a brief paper in 1912, however, Gortner[10] reports on a more fundamental difference between the insoluble melanin from black feathers, black rabbit hair and brown horse hair, and the soluble melanin from black wool and brown horse hair. The former yielded some 3% ash consisting largely of iron oxide, while the latter yielded little or no ash. This seems to demonstrate a difference in chromogens in at least these cases. But even here black pigment may consist of a mixture of melanins containing iron and melanins which do not, derived perhaps from the same chromogens as those which under other conditions produce yellow.

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[4] Hooker, D., 1915. *Anat. Rec.*, 9: 393.
[5] Onslow, H., 1915. *Proc. Roy. Soc.*, B-89: 36.
[6] Lloyd-Jones, O., 1915. *Jour. Exper. Zool.*, 18: 453.
[7] Davenport, C. B. and G. C., 1909. *Amer. Nat.*, 43: 193.
[8] Durham, F. M., 1904. *Proc. Roy. Soc. London*, 74: 310.
[9] Gortner, R. A., 1911. *Biochem. Bull.*, 1: 207.
[10] Gortner, R. A., 1912. *Proc. Soc. Exp. Biol. and Med.*, 9:3.

The chemical difference which Gortner found suggests that the presence of iron bearing chromogens may be the thing which is determined by Mendelian factors for black as opposed to yellow. Such a view, however, is not in harmony with certain other results. Miss Durham[11] found an enzyme difference in the skins of black and yellow guinea-pigs. Onslow[12] was unable to confirm Miss Durham's results, but also found an enzyme difference. He was able to extract a peroxidase from the skins of black rabbits but not from yellow rabbits. It seems unlikely that the same factor should determine both the presence of a particular chromogen and of a particular enzyme. One way to reconcile Gortner's and Onslow's results is to suppose that a feebly acting enzyme oxidizes certain chromogens in the cell giving the appearance of yellow. In the presence of a more powerful enzyme these chromogens and also others (including some containing iron) are thoroughly oxidized yielding sepia granules. Such a view fits in excellently with our knowledge of the relations of the colors in heredity.

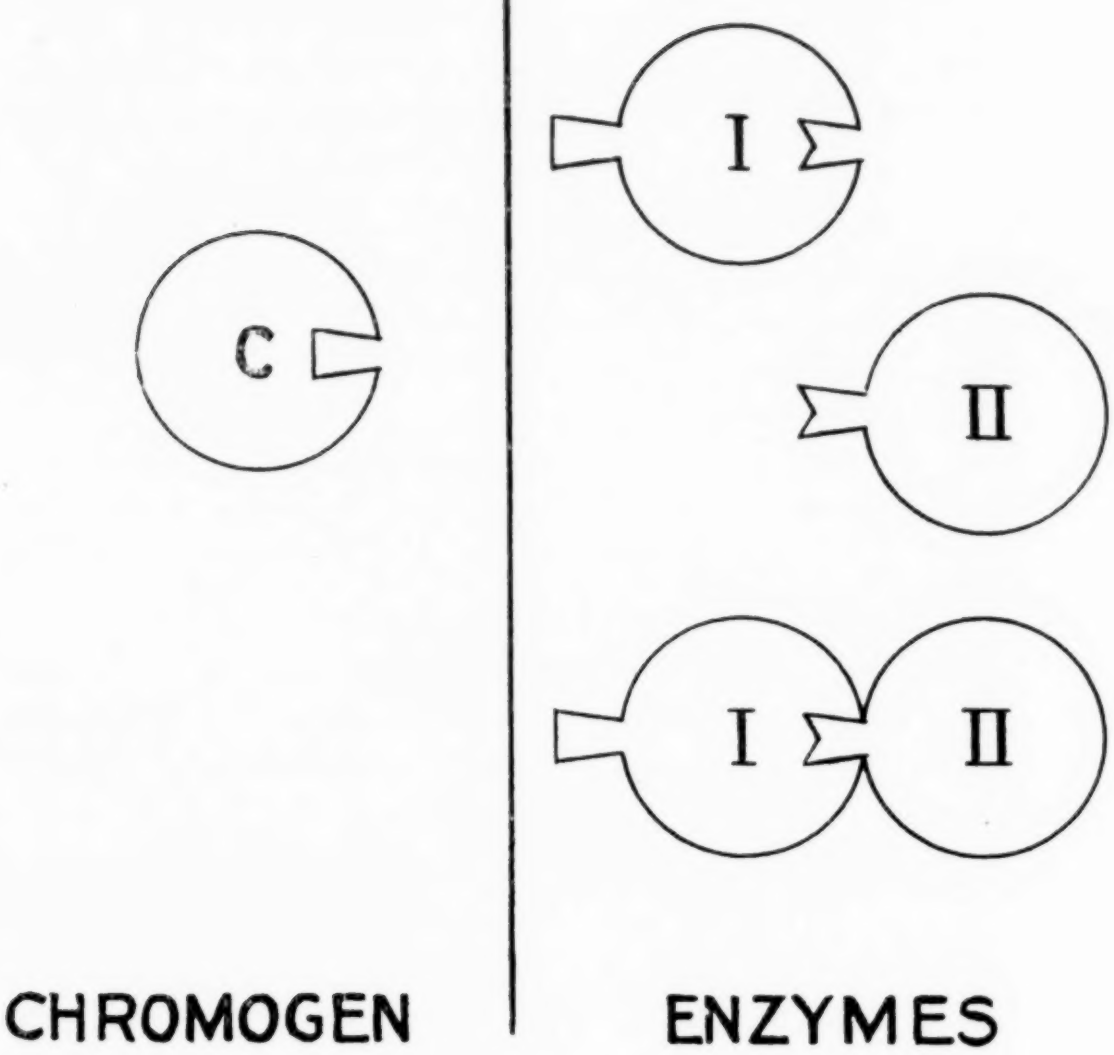
The processes which yield black and yellow are not independent of each other. Both may be reduced or inhibited by the same factor. Onslow investigated several such cases in rabbits. He was able to extract peroxidases from the skins of black, blue and gray rabbits which in the presence of hydrogen peroxide would convert tyrosin into dark pigments. He was unable to extract such enzymes from the white parts of Dutch rabbits and from albinos, both recessive whites. In both cases (as well as in the case of yellow rabbits) the addition of tyrosinase from another source to the solution of extract and tyrosin enabled pigment to develop. As the Dutch pattern and albinism affect yellow and black stocks of rabbits alike, it is evident that our feeble enzyme for yellow and the powerful one for black must contain some common element the loss of which prevents either kind of pigmentation. Thus in different animals of a stock or in different areas on the same animal black and red tend to be intense, dilute or absent alike. But in the same area, there is, in general, a reciprocal relation. Black and red, it is true, may be present together as in reddish-brown human hair and brown horses, but in most cases black obviously increases at the expense of red. This demonstrates either a common chromogen or a common enzyme element or both in the production of black and yellow. More will be said of these relations later.

We have noted several very different kinds of color variations which Onslow has shown to be due to hereditary differences in the enzyme element of the reaction, viz., recessive yellow, albinism, and a recessive white pattern. In two other kinds of variation he obtained a result similar in this respect. In the white parts of English rabbits and in the white belly of gray rabbits—the former due to a dominant factor for white pattern, the latter to a dominant factor for yellow pattern (the agouti factor)—he was not only unable to extract oxidizing enzymes, but found positive inhibitors to be present which prevented pigment production when peroxidases from other sources were added. Gortner[13] has shown that certain chemicals actually have an inhibitory effect on the reaction of tyrosinase with tyrosin and suggested the bearing on the problem of dominant whites. The point of most interest here is that color variations of nearly every kind have been shown to be due genetically to variations in the enzyme element of the reaction which produces pigment.

HYPOTHESIS

The chemical and histological investigations indicate: first, that melanin is produced by the oxidation of certain products of protein metabolism by the action of specific enzymes; second, that this reaction takes place in the cytoplasm of cells probably by enzymes secreted by the nucleus; third, that various chromogens are used, the par-

[11] Durham, F. M., *loc. cit.*
[12] Onslow, H., *loc. cit.*
[13] Gortner, R. A., 1911. *Jour. Biol. Chem.*, 10: 113.



I. Basic enzyme for color production. Acting alone on chromogen, produces yellow.

II. Supplementary to I. Has no effect alone, on chromogen or yellow pigment.

I–II. Oxidizes chromogen to sepia. Effective below threshold level for enzyme I alone. Above this level I and I–II compete. (Fig. 8.)

ticular ones oxidized depending on the character of the enzymes present, and finally that hereditary differences in color are due to hereditary differences in the enzyme element of the reaction. The following provisional hypothesis is built around these considerations:

First, we will suppose that color depends on the rates of production or of potency of two enzymes. Enzyme I is essential to the production of any color, but by itself only produces yellow. Enzyme II is supplementary to enzyme I, producing no effect by itself. The compound enzyme, I–II, produces a darker kind of pigment than enzyme I alone, viz., sepia. Enzyme I–II is also more efficient than enzyme I in another way. It produces sepia pigment even when enzyme I is at too low a potency to produce any yellow by itself. Above the level at which enzyme I produces effects, the two enzymes, I and I–II, compete in the oxidation of chromogen. Chromogen which is oxidized by enzyme I to yellow pigment is incapable of further oxidation to black. In the mixture the presence of the relatively pale yellow color serves mainly to dilute the color of the hair. This production of yellow reduces the amount of dark pigment and the apparent intensity of color, both by reducing the amount of enzyme I which can unite with II to form the enzyme for black production and also by using up chromogen which would otherwise become black. That tyrosinase is exhausted in the production of pigment has been shown by Gortner,[14] who also quotes experiments by Roques (1909) to the same effect.

There are three points in the diagram (Fig. 8) at which physiological processes may affect color-production independently, viz., by influence on chromogen, on enzyme I, and enzyme II. In the first two cases color should be modified regardless of its quality. But as there is as yet no experimental evidence that genetic factors determine variations in the chromogen element it will be convenient at present to consider all such cases as due to influence on enzyme I.

The relations between black, red and white in this scheme are obvious. Inhibition of enzyme II when enzyme I is present gives red. Inhibition of enzyme I gives white regardless of

[14] Gortner, R. A., 1912. *Proc. Soc. Exp. Biol. and Med.*, 9: 1.

whether enzyme II is present or not. The intergrading colors must be looked upon as resulting from reductions of various kinds in the activity of the enzymes. We have recognized two distinct types of intergrades between black and red, the coarsely granular type of bays and sooty yellows, and the finer type of chocolate browns. A mere reduction in quantity of enzyme II may perhaps be thought to result in an intermingling of black and red granules as one or the other of the respective enzymes chances to predominate, while a uniform reduction in potency in some other way not involving a reduction in quantity may give the chocolates and the pale browns of the pink-eyed rodents, in which there seems to be little more tendency for red to win in competition than in intense blacks. Similar relations with respect to enzyme I may account for the differences between the maltese and sepia types of dilution of black and the correlated light red and cream types of dilution of red. Of course, any such definite assignment of physiological effects to factors is at present to be taken mainly as a means of visualizing their action in our ignorance of the real physiology. In order to make wholly clear the relations supposed to hold between the different colors on the hypothesis, the accompanying diagram (Fig. 9) is given. Full quantity is represented by two symbols, reduced quantity by a single symbol, reduced potency by a symbol of small size, and complete inhibition or impotency by absence of symbol. Variations in enzyme I are given horizontally, variations of enzyme II vertically.

The classification of color factors which it is desired to present is based primarily on the difference between factors which act as if on enzyme I, and those which act as if on enzyme II. A secondary classification is based on the mode of action. There is a wide difference between factors which produce no effect in parts of the coat though with maximum effect in other parts, *i.e.*, bring out a pattern, and factors which produce the same effect throughout fur, skin and eyes. In the former case increase in the array of factors causes extension of the pattern; in the latter whatever pattern may be present tends to be stationary on increase in the array of factors. There is instead a further general change in intensity. The coarsely granular types of intergrades should perhaps form a third subclass in each main class, but for the present they are most conveniently put with the pattern factors. They can be considered as determining a fine pattern within the individual hairs.

CLASSIFICATION OF COLOR FACTORS

1. Factors which affect distribution and intensity of color, largely irrespective of the kind of color. (Act as if on enzyme I).

(*a*) Factors which affect the distribution of color in contrast with white.

(*b*) Factors which affect the intensity of color in all colored areas of the skin, fur and eyes.

2. Factors which affect the distribution and intensity of differentiation from yellow to black—effects, of course, visible only in colored areas. (Act as if on enzyme II.)

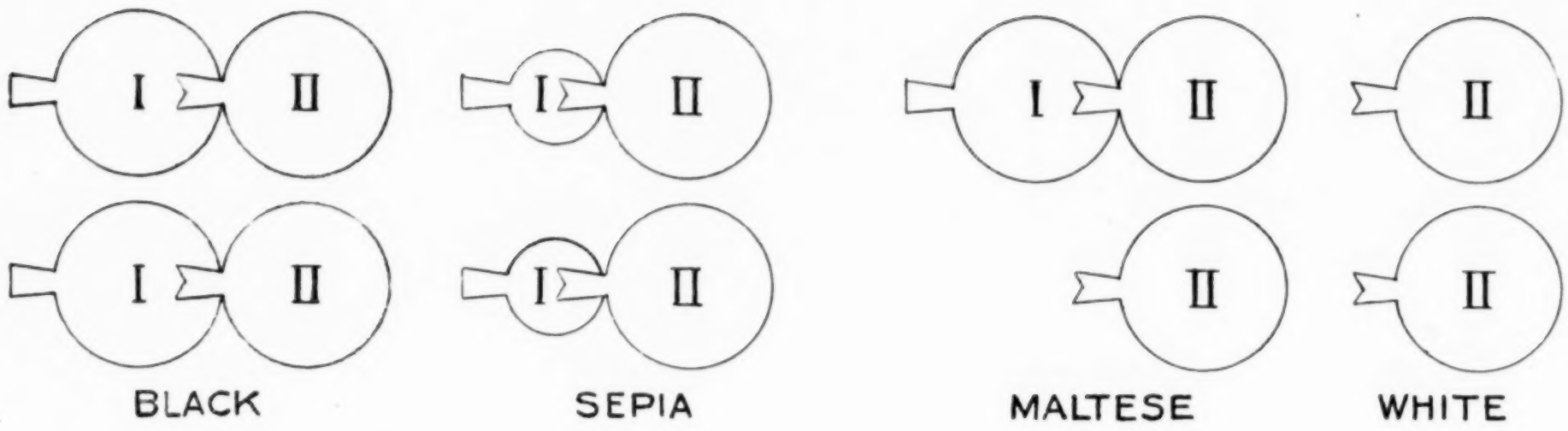
(*a*) Factors which affect the distribution of a dark color (black, sepia, brown, etc.) in contrast with a yellow.

(*b*) Factors which affect the intensity of only the dark colors with effects visible wherever such colors develop in skin. fur and eyes.

This classification differs slightly from one previously advanced by the writer[15] in that classes 2 and 3 of the earlier paper are brought more closely together as classes 2a and 2b.

As an illustration of the classes of factors, consider a guinea-pig which is like a solid black except for the following factors: Σ_w C_d C_d AAbb. Σ_w represents unanalyzed hereditary factors of class 1a which determine a pattern of white regardless of anything else. Factor A of class 2a puts a yellow band in each colored hair. Factor C_d of class 1b makes the yellow a dilute yellow instead of red, and makes the dark parts of the hair lighter than otherwise and perhaps

[15] Wright, S., 1916. Carn. Inst. Wash. Pub., 241, part II.



PRODUCTION OF COAT COLORS IN MAMMALS

The inherited color factors can be classified as if acting on one or other of two enzymes. For explanation see text. (Fig. 9.)

slightly dilutes eye color. Finally factor b of class 2b further modifies the sepia in the coat and eye producing light brown but does not affect the yellow. The animal is a brown-eyed light brown agouti with yellowing ticking and a white pattern in the coat.

It is often difficult for one who is not working in the inheritance of coat color to understand just what color is supposed to be determined by a given array of factors. Probably this can be done most easily by considering the factors in the order just given. First are the factors of class 1a which determine patterns of color and white. No factors considered later can change these white areas. Next to be considered is the pattern of dark and yellow colors visible in the colored areas. These are determined by class 2a. Finally the kind of yellow in the yellow areas may be seen by noting the factors of class 1b and the kind of dark color in the remaining areas by a simultaneous consideration of classes 1b and 2b. Eye color is generally determined wholly by these last two classes, but occasionally extreme white patterns of class 1a invade the eye.

DISCUSSION OF CLASSES OF FACTORS[16]

Class 1*a*.—White patterns are very common in mammals and most of them are obviously determined by factors of this class even where the mode of inheritance has not yet been thoroughly analyzed. The factors which determine the white face of the red Hereford cattle are a good example. The same white face appears in the black cattle from the cross of Hereford with Aberdeen-Angus. Evidently the factors involved strike at color in general regardless of its quality. The same is true of the different types of white patterns found in roan and in white Shorthorns, in the black and white Holsteins, and in Dutch belted cattle. The common white patterns of horses, dogs and cats are similarly independent of the ground colors of the animals. This seems to be true of the belt in Hampshire hogs, but is not so certain in other white patterns in hogs which may correspond to extreme dilution of yellow patterns. One or more recessive Mendelian factors have been demonstrated for the patterns of piebald mice, hooded rats, and Dutch rabbits, while a dominant factor is responsible for the English pattern of rabbits and the white blaze in man.

The mechanism by which such patterns are determined is interesting to speculate upon, but very little is yet known. In the case of the English rabbit, Onslow has demonstrated the presence of an inhibitor which prevents the oxidation of tyrosin by tyrosinase. Apparently the power of a cell to produce this inhibitor is determined by a variety of conditions of which the level of the English factor (absent, heterozygous or homozygous) is one and differences brought about in regional differentiation another' As a result of the combined effects of these conditions a given cell either has no power to produce the inhibitor or can produce sufficient to inhibit any intensity of color. The extent of white patterns seems to be the same in general whether the ground color is intense or dilute. In Dutch rabbits Onslow found no enzyme inhibitor but simply an absence of peroxidase. Here we must suppose that some essential condition in the cells for production of enzyme I is determined by the array of recessive white pattern factors in conjunction with regional differentiation.

The maltese type of dilution which appears under the microscope in such a case as the blue rabbit as due to an alternation of colorless spaces with intense pigmentation within each hair is put provisionally in class 1a. Recessive factors which determine simultane-

[16] Most of the statements in regard to color inheritance are based on well-known investigations. A very detailed review of the literature to 1913 is given by Lang, 1914 (*Experimentelle Vererbungslehre*, pp. 467–888). A discussion of our present knowledge on the subject with extensive bibliography is given by Castle, 1916 (Genetics and Eugenics). The writer may say that all of the statements in regard to guinea-pigs can be based on his own experience, and he has also had the opportunity of becoming directly acquainted with the mode of inheritance of most of the color varieties among rats, mice and rabbits as an assistant in Professor Castle's laboratory for three years. Only a few references are cited in this paper.

ously maltese dilution of black and the homologous kind of dilution of yellow have been demonstrated in dogs, cats, mice and rabbits.

Class 1*b*.—Correlated dilution of black and yellow is probably very common in mammals. A case which seems to be dominant is found in the factor by which dun, mouse and cream-colored horses differ from bays, blacks and chestnuts respectively. An imperfectly dominant factor differentiates dun and yellow cattle from blacks and reds.[17] The sepia and yellow guinea-pigs differ from black and red ones by a unit recessive factor.[18] There are two more allelomorphs of this dilution factor. In red-eyed dilutes yellow disappears entirely, giving place to white, and eye color becomes distinctly dilute while in the lowest recessives of the series—the albinos—sepia as well as yellow nearly disappears and the eyes become pink.

Rats show a series of three allelomorphs which seem to be comparable to the guinea-pig albino series.[19] The lowest recessive determines complete albinism while the second member of the series is much like red-eyed dilution in guinea-pigs. Black is diluted, yellow is reduced to white and the eye color to red. Rabbits show a series of three allelomorphs in the complete albino, Himalayan albino and fully colored varieties. Albinism is found in many other mammals and always seems to be recessive in inheritance. There are a number of curious features in the albino series in guinea-pigs which have had much to do with shaping the hypothesis advanced here. The table below shows roughly the model grades of intensity of yellow and black fur and eye color found with each of the ten possible zygotic formulae. Guinea-pigs of these ten formulae can easily be distinguished by the results of crosses with albinos, the lowest recessives. The full evidence has been given in a recent publication.[20]

	Yellow fur	*Black fur*	*Black eye*
CC	Red	Black	Black
C^d	Red	Black	Black
C_r	Red	Black	Black
C_a	Red	Black	Black
C^dC^d	Yellow	Dark sepia	Black
C^dC_r	Cream	Dark sepia	Black
C^dC_a	Cream	Light sepia	Black
C_rC_r	White	Dark sepia	Red
C_rC_a	White	Light sepia	Red
C_aC_a	White	Sooty white	Pink

There are a number of ways in which such a series of four allelomorphs as C, C^d, C_r and C_a can be interpreted. Complete linkage could explain the mere ratios obtained in crosses but leaves wholly unexplained the graded series of physiological effects. Four diverse non-linear variations of a factor would be another possibility. It seems most in harmony with the broad facts of the series, however, to consider these as four levels in potency of some one factor. But with this interpretation two peculiarities of the series stand out at once. First, we get complete albinism in yellow parts of the fur at a level in the series (C_rC_r) at which black in fur and eye is still quite intense. This renders it unlikely that black results from the further oxidation of yellow pigment or the reverse. The hypothesis suggested is that the efficiency of enzyme I, the basic enzyme for color production but which produces only yellow when acting alone, is increased by union with enzyme II so that black pigment is produced at a much lower threshold than yellow. The second curious fact is the bimodal curve of intensity in black fur in passing down the series of zygotic formulae. If C_d C_a determines a higher potency of enzyme I than C_rC_r, it would seem that it should determine a higher intensity of color everywhere. Yet C_dC_a gives a distinctly paler black than C_rC_r but a more intense yellow and eye color. It will be noticed that this irregularity occurs just at the point at which yellow is able to appear and the explanation suggested is that competition of enzyme I with the

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[17] Wilson, J., 1909. *Sci. Proc. Roy. Dub. Soc.*, 12: 66.
[18] Castle, W. E., and S. Wright, 1916. Carn. Inst. Wash. Pub., 241.
[19] Whiting, P., 1916. *Sci. N. S.*, 43: 781.
[20] Castle, W. E., and S. Wright, *loc. cit.*

enzyme for production of black, I–II, begins at this point and is able to reduce the intensity of the black produced. Both the available quantity of chromogen and the available quantity of enzyme I are reduced in the production of the relatively pale yellow color. In the eye no factor ever brings out yellow, and perhaps enzyme I is at a much lower level than in the fur.

The different thresholds of black and yellow are attested by a great number of facts. In the dilute rats and Himalayan rabbits as well as in the red-eyed dilute and albino guinea-pigs, black is able to develop but not yellow. In many animals with black and red phases, white patterns appear in the red phase which are absent in the black phase. The white belly of the red fox contrasted with solid sepia of the silver phase is an example. A similar example in rabbits will be discussed later. Again climatic changes in pelage follow the same law. Squirrels and hares lose the yellow in their fur in winter before they lose black. Examples of the competition between black and yellow are discussed under class 2a.

Class 2a.—Factor differences of this group are very common. The factors by which red cattle and swine, bay horses, tabby and yellow cats, bicolor and red dogs; agouti, tortoise and yellow rodents, differ from the blacks in each species are examples.

The agouti factor of rats, mice, guinea-pigs, rabbits, cats, and other animals is an interesting example. In all cases agouti is dominant over the absence of the pattern in blacks, browns, etc. Onslow was able to extract a substance which inhibits the oxidation of tyrosin by tyrosinase, from the white belly of gray rabbits, where the agouti factor removes all black from the hair. Onslow compared the case with the enzyme inhibitor which he found in English rabbits but on our interpretation, the latter was an inhibitor of enzyme I, the former of enzyme II. Since only one genetic factor is involved, it seems likely that the same cause which modifies a solid black rabbit in such a way that yellow ticking appears on the back is responsible for the white belly. According to the hypothesis presented here, white appears on the belly when black is inhibited not because there is a general inhibition of pigment production but because enzyme I is below the threshold for the appearance of yellow. There is a parallel case in the white bellied agouti mice. In this case, however, it is possible to increase the general intensity of pigmentation in the animal so that yellow appears on the belly. In agouti guinea-pigs the belly is normally yellow but paler than the back. Such white patterns as those of the gray rabbit and white-bellied agouti mouse illustrate the possibility of confusing white patterns due really to yellow pattern factors of class 2a acting where enzyme I is below the yellow threshold with white patterns of class 1a. It is likely that many dark-eyed whites among mammals are of the former kind. The polar bear is probably an example.[21]

It has been mentioned that the extent of white patterns seems to be independent of the intensity of color due to enzyme I. A parallel statement cannot be made of the agouti pattern. The latter is greatly modified in extent by conditions which have differential effects on the production of black and yellow. In pink-eyed guinea-pigs with a much reduced potency of enzyme II, the agouti band is greatly widened. On the other hand, the agouti band in ordinary intense guinea-pigs can be greatly reduced by crossing with exceptionally intense blacks. Punnett's density factor in rabbits[22] eliminates the agouti pattern altogether. It is also more effective in the ordinary black agoutis than in brown agoutis. Thus the agouti factor seems to determine a certain quantity of inhibitor which is not as a rule sufficient to eliminate all black and the effect depends not merely on the level of the agouti factor but also on the level of potency or quantity of the substance to be inhibited. The dominant agouti factor (A) and the recessive

[21] Lang, A., 1914. *Experimentelle Vererbungslehre.*
[22] Punnett, R. C., 1912. *Jour. Gen.*, 2.

factor of sooty yellow rabbits (e) make an interesting contrast between two factors of class 2a. In the former case, as we have seen, Onslow demonstrated that an enzyme inhibitor was produced, in the latter he was simply unable to demonstrate peroxidase, indicating a reduced quantity or potency as compared with blacks. The following table shows the effects produced by these factors when added to those of a solid black rabbit (aaEE):

	aaEE	*AAEE*
Back	Black	Black ticked with yellow
Belly	Black	White
	aaee	*AAee*
Back	Sooty yellow	Clear yellow
Belly	Black	White

The case can readily be understood if we suppose; first, that both enzymes I and II are strong on the back but feeble on the belly in all rabbits due to a regional differentiation. We will suppose that enzyme I is below the yellow threshold on the belly. Second, we will suppose that factor A determines the production of an inhibitor with the same subtraction effect on enzyme II everywhere, while factor e determines a general proportional reduction in rate of production of enzyme II. On this basis it follows that factor A produces a partial inhibition of black on the back, revealing yellow but a complete inhibition of black on the belly where, however, only white can be revealed. Factor e reduces black on the back sufficiently to permit yellow to predominate in competition while on the belly, where there is no competition from yellow, what little of the black producing enzyme I-II is produced is fully effective and black, or at least blue, results.

Class 2b.—The factors which reduce the intensity of black areas in skin, fur and eyes without affecting red areas form a clearly defined class. The brown-eyed chocolate mice, guinea-pigs and rabbits; the pink-eyed pale sepia or "lilac" mice, guinea-pigs and rats, and the red-eyed rats of similar coat color[23] differ from blacks by factors of this class. Among the larger animals the difference between liver-colored and black dogs seems to be of this kind. Probably chestnut and liver-colored horses differ from bays and blacks by such a factor. All of these factors are recessive. In the pink-eyed mice, guinea-pigs and rats it is remarkable to what an extent black is diluted without bringing out any distinctly reddish tinge although in red regions of the fur as in the agouti band of gray varieties the red appears in full intensity. There is evidently a different sort of reduction of enzyme II from that in the sooty yellow rabbit. A normal quantity of enzyme II but reduced potency in some other way would seem to be required in class 2b.

SIMULTANEOUS EFFECTS

It has been assumed so far that factors act only on one or the other of the hypothetical enzymes I and II. In the great majority of cases this is satisfactory but it is not impossible that a factor may influence both enzymes in the course of development. In fact the writer will soon publish evidence on one such case in guinea-pigs. Tri-color male guinea-pigs of many different stocks agree in showing a slightly greater average area of color as opposed to white than their sisters, and they also show relatively more black as opposed to red. Maleness seems to determine a higher level of both enzymes I and II as regards pattern. The effect on color is perhaps due rather to a general metabolic difference in the cells of males and females early in ontogeny than to any specific modes of action on the two enzymes. The same may be true of certain coat patterns in which it seems necessary to suppose that the level of enzymes I and II is raised or lowered simultaneously in some respect by regional differentiation. We have cited the cases of the rabbit, mouse, and guinea-pig in which it was found con-

[23] These red-eyed rats first described by Castle (1914, *Amer. Nat.*) under the name of yellows must not be confused with the red-eyed rats described by Whiting (*loc. cit.*). In the former yellow pigment is unaffected and to a large extent gives the color to the fur in agoutis, owing to the great reduction of black. In the latter, yellow is reduced to white, while black is only slightly affected.

venient to suppose that both enzymes I and II are strong on the back and weak on the belly. Similar cases are common. Another sort of example seems to be present in the tiger pattern of cats. In yellow cats the pattern is shown by alternate orange and cream stripes which on our interpretation must indicate alternate stripes of high and low potency of enzyme I. In tabby cats, the intense stripes are solid black, the pale stripes show yellow ticking which seems to require that enzyme II also be strong in the former, weak in the latter.

CONCLUSION

In the present paper an attempt has been made to relate the findings of the biochemist in regard to melanin pigment with the great mass of curious relations between colors which have come to light in genetic work. A scheme is given which is designed to show the inter-relations of the different mammalian coat colors and a classification of color factors is suggested. It is hoped that these will be of use in organizing our present very extensive knowledge of color inheritance and in aiding in the discovery of new facts, or at least in leading to a better scheme and classification.

Finally the bringing under one point of view of biochemical and genetic facts would have great intrinsic interest. The present paper attempts merely to trace the character—coat color—back one stage in development. Instead of considering factors as acting on this one character, they have been divided into two sets acting on two characters, production of the hypothetical enzymes I and II. Suggestions have been made in certain cases in regard to further tracing back of the action of the factors. A more thorough comparison than has yet been made of the effects of factors in all combinations should yield much data bearing on the process of pigmentation and give a very much more complete understanding of the heredity of color than we have at present. By constant comparison of the deductions from such work with the findings of the biochemist, it should be possible in the end to establish a very pretty correlation of results.

Does Racial Intermarriage Lead to Sterility?

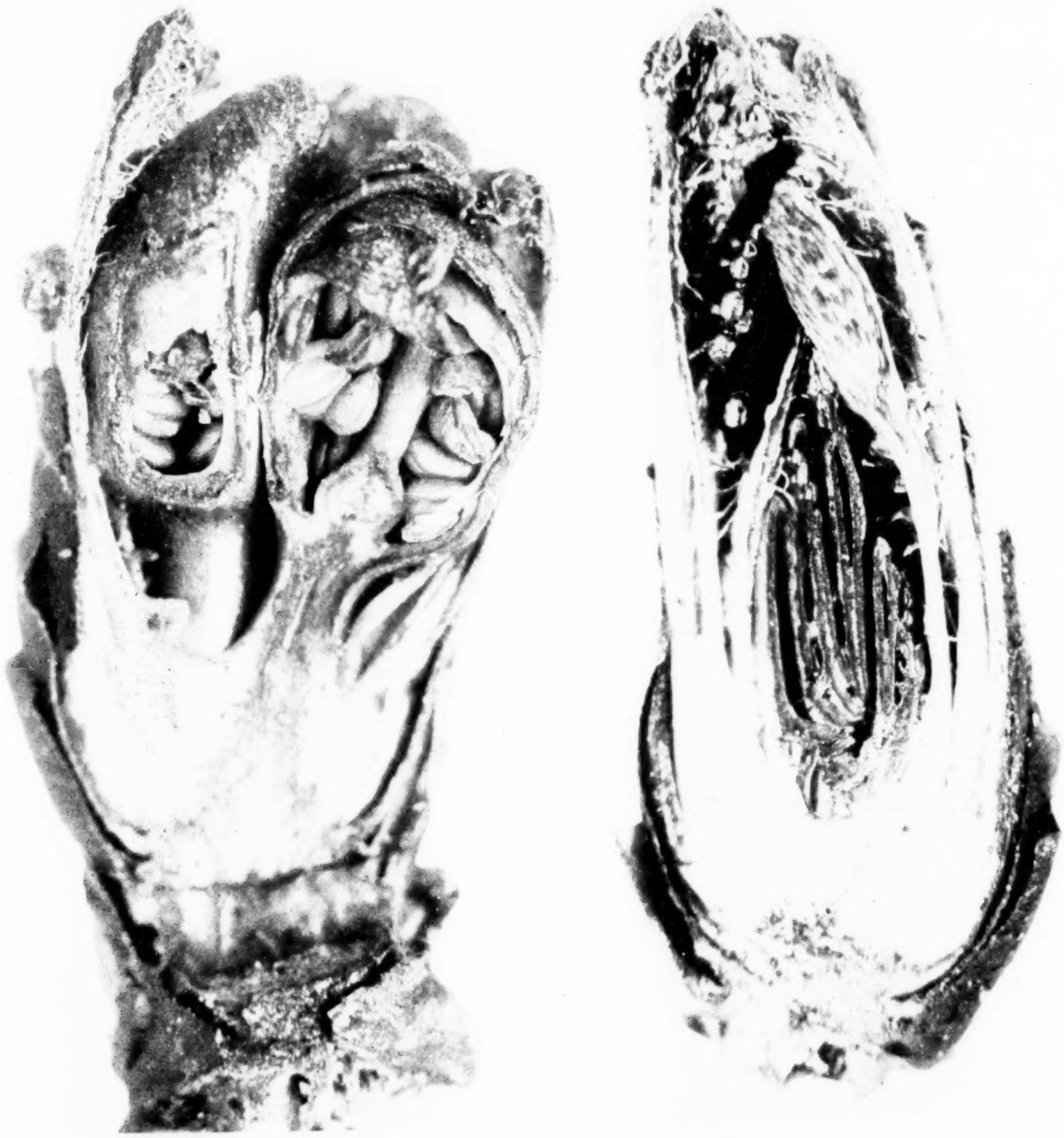
That the intermarriage of different races leads to diminished size of family is the conclusion of Prof. Albert Ernest Jenks of the University of Minnesota. His studies in Minneapolis, Minn., Sioux Falls, S. Dak., and in Lincoln County, Minn., convince him that "human hybridization is a powerful factor in America, that it does affect fecundity—being a process toward the gradual numerical weakening of the groups amalgamating. It is thus an increasing factor in America, affecting fecundity to the greatest extent in those families most completely amalgamated." He adds that "as yet the 'American' is not a pure-bred ethnic group but is an extremely amalgamated group, and, in consequence of the amalgamation, is a decidedly impotent group." His investigations are summarized in the Holmes Anniversary Volume.

A Valuable Variety of Barley

The introduction of the single improved variety of barley called "Plumage" has added at least $1,250,000 a year to the value of the English barley crop, according to the estimate of the British Board of Agriculture. Wheats produced by the Institute of Plant Breeding at Cambridge have also made a notable contribution to the national wealth. Little has been done in England, the board complains, to improve the varieties of roots, rotation grasses and clovers, or any of the minor field crops.

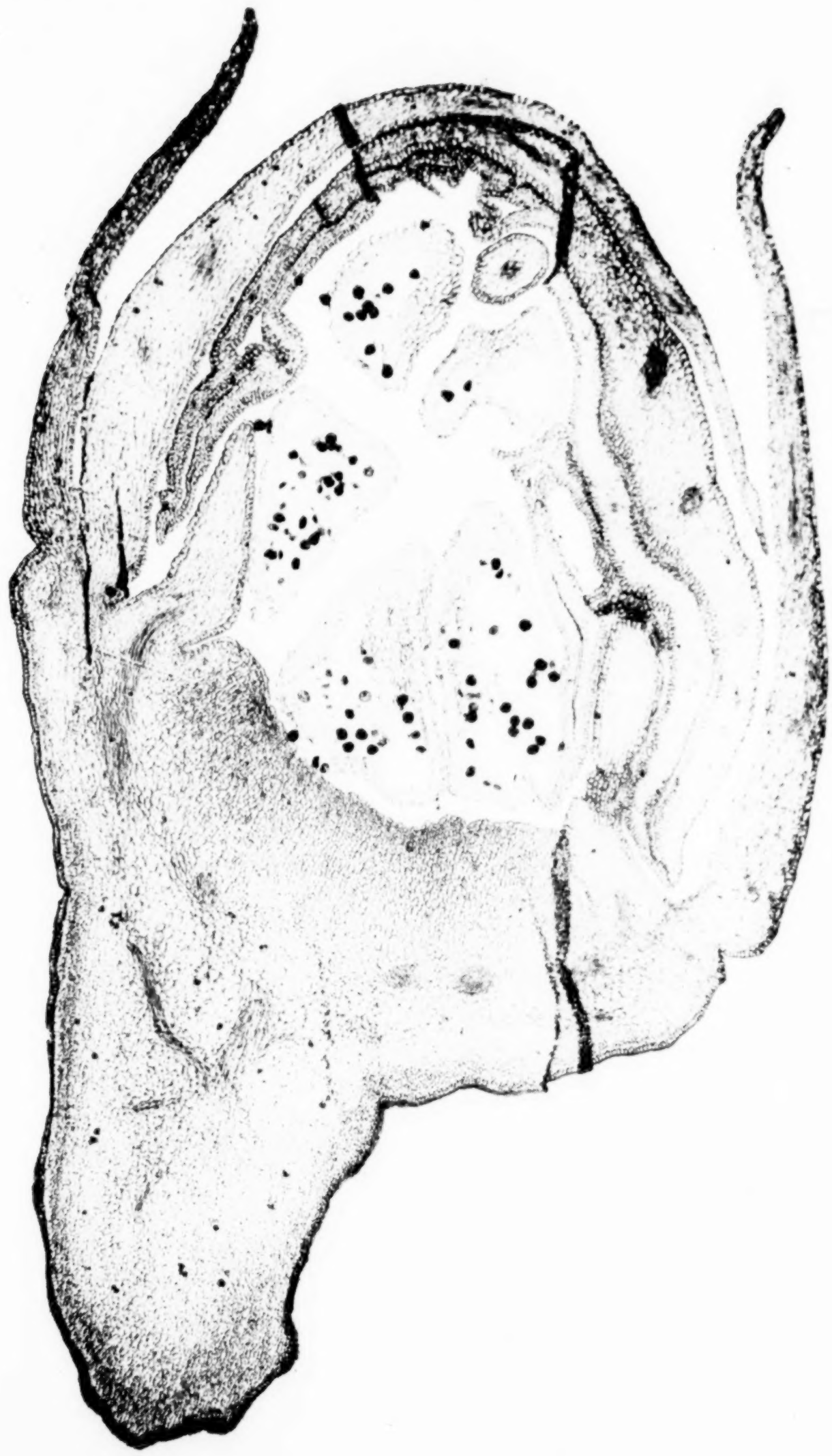
FLOWER BUDS AND LEAF BUDS

Buds which produce only leaves, and these which give rise to flowers and fruit, are quite distinct in most plants, but differ in appearance from species to species. Usually the flower buds are considerably the larger. The pear, shown above, has its flower buds on short spur-branches (at the left) while its leaf buds (at the right), are borne directly on the branch. Photograph, twice natural size, by John Howard Paine. (Fig. 10.)



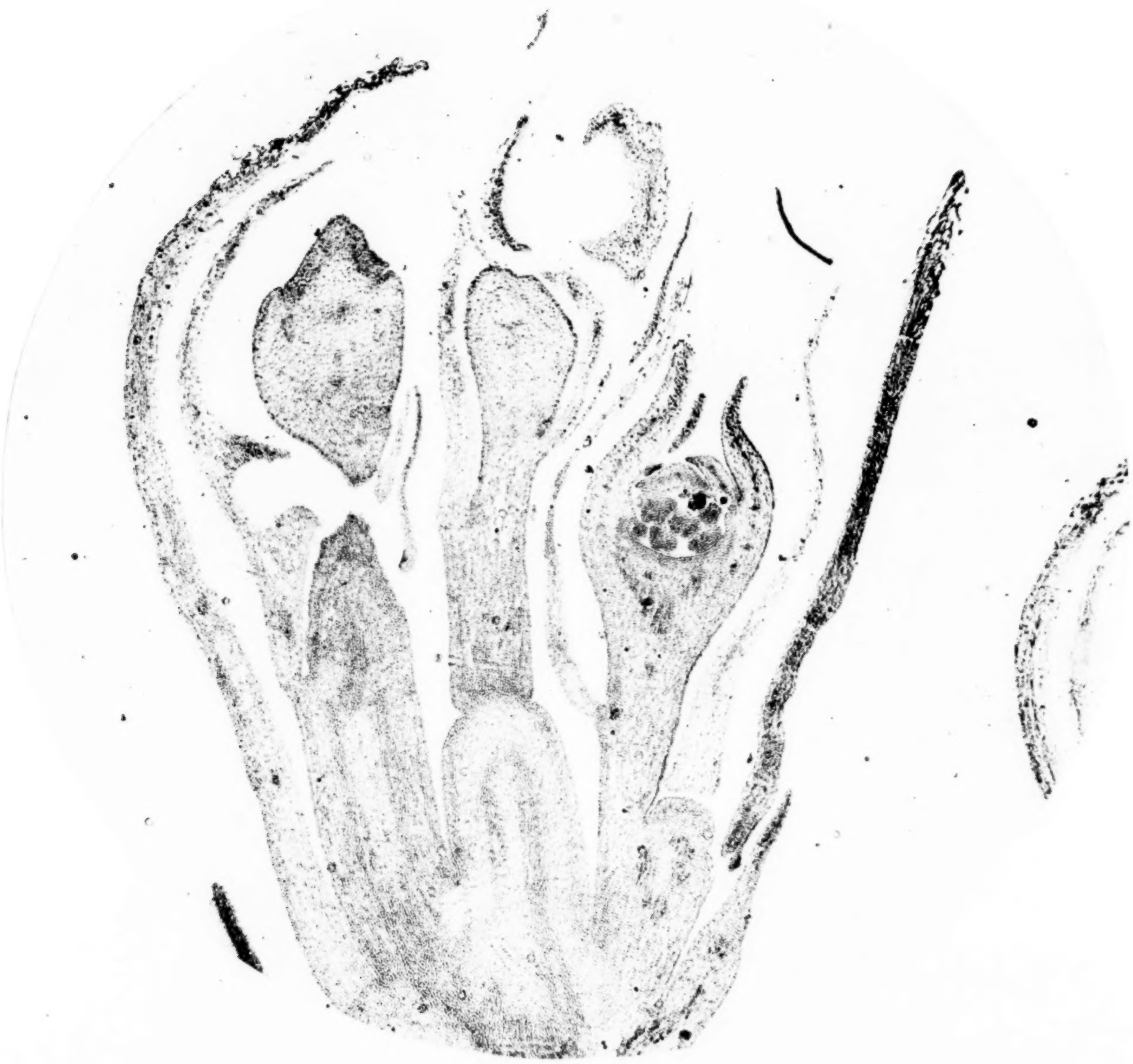
SECTIONS OF CHERRY BUDS

The surest way to tell whether a bud contains leaves or flowers is to slice it open lengthways with a sharp knife. The cherry buds shown above have been enlarged 15 diameters. At the left is a flower bud. In the cherry, two, three or four flowers are enclosed in a single bud; in this case two flowers can be seen, the conspicuous sacs being the anthers filled with pollen-grains. At the right is a leaf bud which shows nothing except tightly folded leaves. In some cases, such as the apple and Norway maple, a single bud encloses a miniature shoot bearing both leaves and flowers. Photograph by John Howard Paine. (Fig. 11.)



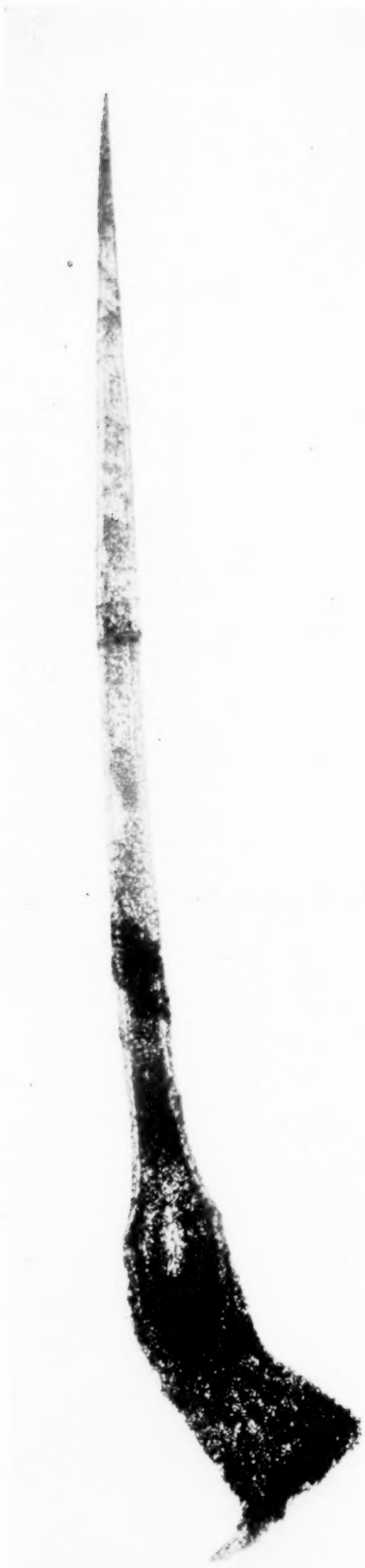
LONGITUDINAL SECTION OF A HAWTHORN FLOWER BUD

When a thin slice of a hawthorn flower bud is placed under the microscope, its structure is revealed clearly. The anthers have been cut through, and the pollen-grains within them stand out sharply as little black dots. The scales which cover the bud on the outside are modified leaf-parts. Photomicrograph by John Howard Paine. (Fig. 12.)



LONGITUDINAL SECTION OF A LEAF BUD

The bud is a very important organ of the plant, and from the young and tender nature of its parts is very susceptible to injury. This is especially true of the "resting buds" of northern climates, which have to survive the winter and are frequently wet and frozen. In tropical climates with plenty of moisture the chlorophyll of the minute leaves might be decomposed by the intense radiation. Buds are carefully protected from these dangers in many different ways, by the older leaves, by scales, hairs, wax, etc. The commonest way is by a modification of leaf-steams to form a relatively hard, smooth, scaly coat. Photomicrograph by John Howard Paine. (Fig. 13.)



A STINGING HAIR

It is a single elongated cell, the walls of which are hardened with silica. Photomicrograph by John Howard Paine. (Fig. 14.)

THE HAIRS OF NETTLES

WHEN you brush against a nettle, you are stung by a very simple weapon. The plant has many fine hairs, each of which is hollow and filled with an albuminoid liquid under pressure. Touch breaks off the point of the hair and leaves, in effect, a tiny hypodermic needle, which injects its contents under the skin, producing a burning sensation that cannot be overlooked.

These stinging hairs, while simple, are of a very specialized character, and at first sight one would feel no doubt that they had some useful part in the plant's life. Otherwise, it might be argued, they would not exist.

ARE THEY USEFUL?

But recent students have strongly questioned this attitude toward nature. In their Text-book of Botany (ii, 577) Coulter, Barnes and Cowles say: "Nowhere in plants is there an organ more clearly fitted for a definite function than are stinging hairs, yet there is no evidence that they are of any special advantage to the plant possessing them. Nothing is known concerning the factors underlying their development, since they neither vary appreciably nor grade obviously into other sorts of hairs."

CANNOT BE DISCARDED

Plants have numerous kinds of hairs, and in some cases it has been found that they are of advantage as a protection from the cold or heat, or to prevent excessive evaporation of moisture. In other cases they do not seem to be of any value to the plant, and may perhaps exist merely as by-products of some part of the plant's evolution. It is likely, the authors above-mentioned think, "that most such hairs are of little or no advantage. The idea should be abandoned that plants have the power to discard organs that are not of use."

Genetics Literature

THE annual reports of the AMERICAN BREEDERS' ASSOCIATION, published in seven volumes, form the most valuable collection of material for students of genetics which has been published in the United States. Most of them are out of print and are becoming expensive. All of them are nearly indispensable to libraries, institutions and students of plant and animal breeding, heredity, variation, eugenics, or genetics in general.

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